The effects of soil type and management strategy on vegetation structure and function in a semi-arid savanna, South Africa

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Declaration

I, the undersigned, hereby declare that the work contained in this thesis 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.

Abstract

Bush encroachment in savannas leads to reduced diversity, productivity and profitability of rangelands. This holds important implications for the livestock and eco-tourism industries, as well as for subsistence ranchers in the South African semi-arid savannas, who depend on this vegetation type for economic and livelihood purposes. Soil moisture, nutrients, fire and herbivory are generally regarded as the principal factors determining vegetation structure and function within savannas. The factors and processes involved in the determination of the tree:grass ratio within savannas are, however, not clearly understood. We investigated the role of soil type and management strategy (cattle, game and communal grazing) in the determination of the presence and distribution of plant species in general, and on the presence and distribution of the encroaching tree species, *Acacia mellifera*, specifically. Both short- and long-term trends were investigated. The study area, the Kimberley Triangle, (Northern Cape Province, South Africa), was ideal for this kind of study because it has different management strategies practised on several soil types, and bush encroachment is a widespread phenomenon.

Contrary to the belief that heavy livestock grazing is the main cause of increases in the tree:grass ratio, we found that soil type, through its effects on plant growth and on the presence and availability of soil moisture and nutrients, is more important in determining vegetation composition than management strategy. It was found that the various types of grazing management mainly influenced vegetation structure and function by affecting the competitive interactions between N_2-fixing woody species and non-N_2-fixing grasses. Of the soil factors affecting vegetation composition, soil texture was a good indicator of the physical conditions for plant growth in an area, and also of the presence and availability of soil moisture and nutrients. We found that sand and clay soils are relatively resistant to bush encroachment as compared to loamy-sand and -clay mixes. This is because woody growth is impaired in the first-mentioned habitats by soil texture, soil moisture regimes and heavy utilisation. In soils with combinations of loam, sand and clay, soil texture and moisture are not limiting to woody growth and if the repressive competitive effect of grasses on woody vegetation is removed, opportunities are created for recruitment of woody species and encroachment. Additionally, rockiness increases soil moisture infiltration. In the study area, woody species, and specifically *A. mellifera*, are associated with these areas. We suggest that

in the study area, rocky areas are naturally encroached. This is in agreement with the patch-dynamic approach to savanna vegetation dynamics. Because soil moisture is such an important factor in the determination of the tree:grass ratio in the study area, we further suggest that in above-average rainfall years, when soil moisture conditions are optimal for woody seed germination, establishment and growth, heavy grazing should be avoided, as it would provide the opportunity for encroachment.

Keywords: Bush encroachment; N_2-fixing species; game, cattle, communal grazing; soil texture; soil moisture; soil nutrients; *Acacia mellifera*; tree-grass competition.

Opsomming

Bosindringing in savanna gebiede het verlaagde diversiteit, produktiwiteit en winsgewendheid van natuurlike weivelde tot gevolg. Behalwe dat dit die Suid-Afrikaanse vee- en eko-toerisme bedrywe raak, is verskeie bestaansboerderye afhanklik van die plantegroei-tipe vir oorlewing. Grondvog, grondvoedingstowwe, vuur en beweiding word algemeen aanvaar as die belangrikste faktore wat die struktuur en funksie van savannas bepaal. Daar is egter nog nie duidelikheid oor die prosesse wat betrokke is in die bepaling van die boom-gras verhouding in savannas nie. In dié studie het ons ondersoek ingestel na die invloed van grond tipe en beweidingstrategieë (beweiding deur beeste, wild, of kommunale beweiding) op die algemene verspreiding van verskillende plant spesies, en ook op die van die indringer spesie, *Acacia mellifera*. Beide kort- en lang-termyn patrone is ondersoek. Die studiegebied, die Kimberley Driehoek in die Noord-Kaap, Suid-Afrika, was ideaal vir so 'n ondersoek omdat verskillende beweiding strategieë op verskeie grond-tipes beoefen word maar bosindringing steeds 'n algemene verskynsel in die gebied is.

Ons bevinding was dat, ten spyte van die feit dat daar oor die algemeen geglo word dat swaar beweiding die hoof oorsaak van bosindringing is, grond-tipe belangriker is in die bepaling van die spesie-samestelling van 'n gebied. Dit is as gevolg van die feit dat grond-tipe die groei van plante beïnvloed deur die teenwoordigheid en beskikbaarheid van grondvog en –nutriënte te bepaal. Die verskillende beweidingstrategieë beïnvloed meerendeels die kompetatiewe interaksies tussen N_2-bindende hout-agtige spesies teenoor nie-N_2-bindende gras-agtige spesies. Grond-tekstuur was 'n goeie aanduiding van die algemene toestande vir plantegroei en ook van die teenwoordigheid en beskikbaarheid van grondvog en –nutriënte. Ons het bevind dat sand en klei grond, relatief tot leem, sand en klei kombinasies, weerstandbiedend is teen bosindringing as gevolg van die tekstuur, water-regimes en swaar beweidings vlakke wat op die grond-tipes voorkom. Omdat grond-tekstuur en grondvog nie beperkend is op die leem-, sand- en klei-grond kombinasies nie, kan bosindringing maklik hier voorkom as die onderdrukkende effek wat grasse op houtagtige plantegroei het, deur swaar beweiding verwyder word. *A. mellifera* is ook oor die algemeen met klipperige gebiede geassosieer omdat klipperigheid lei tot verhoogde infiltrasie van grondvog. In die studie-gebied is klipperige areas dan ook van nature ingedring deur *A. mellifera*. Dit stem ooreen met die siening dat savannas bestaan uit "laslappe" van verskillende plantegroei (patch-dynamic

approach). Dit was duidelik dat grondvog 'n belangrike bepalende faktor is in die bepaling van die boom-gras verhouding in die studiegebied. Ons stel dus voor dat in bo-gemiddelde reënval jare, swaar beweiding vermy moet word, omdat houtagtige saailinge gedurende die tydperke maklik kan ontkiem en vestig juis omdat grondvog dan nie beperkend is nie.

Sleutelwoorde: Bosindringing; N_2-bindende spesies; bees, wild, kommunale beweiding; grond tekstuur; grond-vog; grond-nutriënte; *Acacia mellifera*; boom-gras kompetisie.

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Chapter 1

Introduction

1. General background

The savannas form a framework of life for a vast number of people in the third world, including large parts of southern Africa (Stott 1991). Almost one fifth of the world's population live in savannas (Solbrig 1990), many of them in rural societies that depend on the ecosystem services of this vegetation type for their livelihood (Higgins et al. 1999).

Savannas are one of the world's major biomes, and are the dominant vegetation type of Africa (Scholes 1997). It is also the biome that covers the greatest extent (54 %) of southern Africa, and a third of South Africa (Rutherford & Westfall 1986; Scholes 1997). The importance of savannas lie in:

 (1) the large contribution that they make to the informal and subsistence economies through the supply of grazing, fuel wood, timber and other resources;

 (2) their contribution to the formal economy as the main location of the livestock and ecotourism industries (84 % of land in the savanna biome of South Africa is used for extensive ranching purposes, including cattle, small stock and game animals (Grossman & Gandar 1989));

 (3) their global impact through the emissions of trace gasses from fires, soils, vegetation and animals (Justice et al. 1994; Scholes & Hall 1996);

 (4) the sequestration of soil carbon and biomass (Scholes & Hall 1996); and,

 (5) their biological diversity (Scholes 1997).

The natural savanna and grassland vegetation in the drier parts of Africa probably evolved under light utilization by shifting populations of indigenous herbivores (Kelly & Walker 1976). It has been hypothesised that the structure of savanna vegetation is maintained largely through this association (Noy-Meir 1982; Solbrig et al. 1996; Hoffman & Ashwell 2001). However, since the major introductions of domestic livestock in the late 1800's, when settlement of the drier parts of the tropics and sub-tropics by Europeans was at its peak, the pattern and intensity of utilization of the natural vegetation has changed,

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and a drastic reduction in numbers, or even elimination of indigenous large mammals and herbivores and their predators, occurred in conjunction with the increases in cattle and sheep populations (Walker et al. 1981). The mega-herbivores i.e. elephant, rhinoceros and hippopotamus, and large grazing animals, such as wildebeest, hartebeest and zebra, play key roles in a number of important population and ecosystem processes within the savanna and grassland biomes (Scholes 1997). The removal of these indigenous herbivores and the presence of increasing domestic livestock populations, induces population crashes as the carrying capacity exceeds that of the natural vegetation. Marked changes in the vegetation and a general degradation of the ecosystem prevents recovery of the vegetation and subsequent restocking of the veld, and results in alterations in the fire regime and reduced use of trees. This process of land degradation usually begins with a change in grass species composition, followed by a decline in perennial grass cover, and an increase in the biomass of annual grasses and woody vegetation (Walker et al. 1981; Owen-Smith & Danckwerts 1997).

The consequences of land degradation are manifold and may take many forms. These include soil, water and veld degradation, the latter in the form of alien plant invasions of grazing lands, long-term losses of natural vegetation in the form of loss of vegetation cover and/or changes in species composition, deforestation or bush encroachment. This leads to a loss of biological or economic productivity of an area and is of great concern to rural communities, ranchers and natural resource managers (Hoffman & Ashwell 2001).

2. Land degradation in South Africa – bush encroachment

In this study, the form of land degradation that will be discussed and which is common in the savanna biome, and specifically the study area, is bush encroachment. In 1989 it was estimated that of the approximately 43 million ha comprising the savanna biome in South Africa, bush encroachment had rendered 1.1 million ha unusable, threatening 27 million additional ha and reducing the carrying capacity of much of the rest of the region by up to 50% (Grossman & Gandar 1989).

Bush encroachment, also called bush thickening, is defined as an increase in woody plant density and cover in grassland or savanna ecosystems, with an accompanying change in herbaceous cover and composition of the natural vegetation (O'Connor & Crow 2000;

Hoffman & Ashwell 2001). Savanna structure and function is determined principally by soil moisture, nutrients, fire and herbivory, the latter two factors acting as modifying agents, influencing the availability of and competition for soil moisture and nutrients (Noy-Meir 1982; O'Connor 1985; Skarpe 1992; Teague & Smit 1992; Vetaas 1992; Solbrig et al. 1996). The ratio of the woody to grassy vegetation in semi-arid savannas can be explained by Walter's two-layered hypothesis (Walter 1954; Walker & Noy-Meir 1982). Although this is regarded by many authors to be an oversimplification (Knoop & Walker 1985), it provides a useful theoretical base to understanding the process of bush encroachment. It states that grasses outcompete woody species with regard to water in the upper soil layers, leaving limited amounts to penetrate to the deeper soil layers where it is exclusively available to the woody vegetation. When the grass layer is damaged by e.g. overgrazing, more water becomes available in the deeper soil layers for woody growth. This provides the opportunity for woody species to increase and for certain species to encroach.

Bush encroachment is a relatively recent phenomenon (Hoffman & Ashwell 2001), and has in most cases been attributed to human disturbance in conjunction with rainfall events of optimal intensity and frequency for germination and survival of seedlings of the encroaching species. Heavy grazing by livestock is generally seen as the primary cause of disturbance, followed by the replacement of indigenous browsing animals with domestic livestock and a reduced fire frequency as a result of the removal of the grass layer by continuous grazing (Noy-Meir 1982; Skarpe 1990; Ward et al. 2000; Hoffman & Ashwell 2001). Recently, however, the debate around rangeland degradation by livestock has suggested that climate (especially rainfall) has a greater influence on vegetation dynamics than pastoral systems in semi-arid areas and that vegetation has a high capacity to recover from grazing disturbance (Ellis & Swift 1988; Behnke & Scoones 1993; Ellis et al. 1993; Sullivan 1996).

On a more global scale, climate change (specifically CO_2 enrichment and increased UV-B radiation), in conjunction with the factors discussed above, has been suggested as a reason for the gradual increase of shrubs over a long period of time (Neilson 1986; Bond &Midgley 2001; Gifford & Howden 2001). Research on this aspect has however up to now been sparse and the results sometimes conflicting. It has been proposed that global increases in atmospheric CO_2 concentrations may be driving bush encroachment through the advantageous effects that these increases have on C_3 species (mostly woody) over C_4 species

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(mostly grasses) with respect to physiological activity, growth and competitive ability (Johnson et al. 1993; Polley et al. 1994). Global warming in the form of increased UV-B radiation, on the other hand, may favour C_4 grasses more than C_3 shrub species because the C_4 grasses generally have a higher optimum temperature for photosynthesis (Dukes & Mooney 1999). It is more generally accepted that CO_2 enrichment and increased UV-B radiation alone is not enough to explain the phenomenon of bush encroachment. Global climatic change in conjunction with factors like heavy grazing, and reduced fire frequency might however contribute to explaining this state (Archer et al. 1995; Wand et al. 1996).

3. Consequences of land degradation and bush encroachment

Although bush encroachment can be seen as a natural part of the succession process where vegetation changes from one successional stage to the next (Skarpe 1990; Hoffman & Ashwell 2001), it still has important consequences. Land degradation in general and specifically bush encroachment in savannas, is considered to be a major threat to livestock production and nature conservation in southern Africa and has serious social and economic implications (Milton & Dean 1995). One of the negative impacts of bush encroachment is the effect it has on species diversity, including species richness of savanna ecosystems, due to the transformation of large areas to monoculture stands (Dean et al. 1999). While the significance of species richness for savanna ecosystem function has not been quantified, biodiversity in savannas has been associated positively with productivity, nutrient cycling, water economy, soil properties and ecosystem resilience (Solbrig et al. 1996). Factors associated with bush encroachment i.e. lowered cover and biomass and altered plant species composition of herbaceous vegetation, therefore leads to reduced veld productivity and grazing capacity of the veld (Dean & McDonald 1994). To generate a modest income, rangelands in poor condition need to be four to five times larger than comparable rangelands in good condition (Moore & Odendaal 1987; Danckwerts & Marais 1989). In order to maintain productivity under such circumstances, ranchers need to either increase their land or ranch more intensively by making use of supplementary feed, or try to control the problem, thereby having to invest in fertilizers, pesticides and machinery. Increased production costs feed the inflation spiral and reduce the viability of ranching (Hoffman & Ashwell 2001). A further direct social implication is the altered species composition, decreased biomass and

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decreased species richness associated with increases in woody vegetation, which translates into a reduced range and amount of useful plant products for rural inhabitants, influencing the sustainability of their livelihoods (Higgins et al. 1999).

Further threats posed by bush encroachment in savannas include its effect on wildlife habitat conservation, patchy redistribution of nutrients and water in the soil, soil erosion, and therefore desertification (Walker et al. 1981; Schlesinger et al. 1990; Scholes & Walker 1993). On a global scale, alterations of plant cover and soil processes may further constitute important feedback to climate and atmospheric chemistry (Schlesinger et al. 1990). Furthermore, the reduction in the resilience of the system can lead to increased species losses in the future (Higgins et al. 1999).

4. Rationale and study objectives

In order to manage our country's savanna ecosystems on a sustainable basis, whether it be for conservation, economic or social reasons, we need to understand the processes that drive savanna systems and the effects that different modifying factors have on these processes. Knowledge of the factors and processes governing savanna structure and function is also needed to address problems of land degradation such as bush encroachment. It is, however, often quite difficult to explain the distribution and structure of vegetation at any given time, as it is influenced by many factors that impact the vegetation through its effects on its distribution and structure. Of the factors determining savanna structure and function (soil moisture, nutrients, fire and herbivory), fire does not play a dominant role in semi-arid savannas in general, and specifically in the study area where although fire is an integral part of the savanna system's functioning, fire frequencies are highly reduced because of the management strategies in place in the area. This is due to the low and erratic rainfall regimes of semi-arid areas, which leads to low fuel loads, reducing the frequency and intensity of fires. It was therefore decided to focus on the effects that soil type and grazing strategy has on the vegetation distribution and structure in general and on bush encroachment specifically. These factors are expected to influence vegetation mainly through their effects on soil moisture and nutrient presence and availability and through their effects on the competitive interactions within the system. The study area also lent itself to this approach.

Study area - the Kimberley Triangle

Background

The Kimberley triangle is a 100 000 ha area, situated 25 km west and 61 km north-north west of Kimberley and bordered by the Vaal River to the north and west. It is bounded by the following coordinates: 28° 27' 04'' S, 24° 42' 03'' E, and 28° 44' 05'' S, 24° 41' 00'' E, and lies between 1020 and 1230 m above sea-level (Figure 1-1). It falls within the savanna biome and the vegetation within this area is classified as Kimberley Thorn Bushveld (Van Rooyen & Bredenkamp 1996).

The Kimberley Triangle consists of land owned by the following private landowners, organizations and communities. The land use strategies for each area are given in brackets (Van Riet & Louw 1999).

- The State (Vaalbos National Park. Currently managed by the South African National Parks but soon to be deproclaimed – wildlife conservation)
- De Beers Consolidated Mines Limited (Rooipoort – game ranching and mining)
- The Schmidtsdrift Tswana Community (Schmidtsdrift) (not included in study area)
- The !Xu and Khwe (San) Common Property Association (Platfontein – land rented for grazing, mining)
- The Pniel Community (portion of Pniel – various livestock, mainly cattle, sheep and goats)
- Evangelical Lutheran Church (portion of Pniel – cattle and game ranching, mining)
- Various private ranchers (Doornlaagte, Langverwacht and Quintus, Rust-en-Vrede, Secretarius – cattle and game ranching).

The area therefore consists of land owned by many different groups of landowners, managing their land in different ways i.e. different grazing strategies are practised on soils with different characteristics (Figure 1-1). Bush encroachment has however been identified across the

whole area, to a greater or lesser extent. This provides the ideal opportunity for a relational study.

Additionally, in September 1997, the Kimberley Triangle Forum (KTF) was formed by the landowners in the area, after the opportunity was identified to consolidate the land in the Kimberley Triangle area and develop it into a major eco-tourism attraction that is capable of catering to the local, regional, national and international markets. The KTF was established with the following vision (Van Riet & Louw 1999):

"To establish a co-operative land use area that is managed according to recognized conservation principles within a joint management plan, which optimizes the sustainable use of its natural resources to increase economic activities in the area."

The overriding purpose of such a development would be to stimulate job creation, economic activity and wealth creation through optimal and sustainable use of the natural resource base. The Kimberley Triangle would remain a multiple use area, providing for tourism, the sustainable harvesting of plant resources (agricultural and natural), commercial hunting, grazing and related activities (Van Riet & Louw 1999).

The information obtained from this study will therefore be useful for a better understanding of the patterns and processes existing in this semi-arid savanna ecosystem by individual landowners, and also for the initiative mentioned above. This knowledge can then be employed to develop sound management practices, improving the sustainability of the use and development of the area.

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Legend

Boundaries of farms in the Kimberley Triangle

Land Types

Ae - Red soils with high base status, > 0.3 m deep

Ah - Red and yellow soils with high base status, < 15 % clay

Fb - Lime rare or absent in upland soils, but present in low-lying soils

Fc - Lime present in the landscape

Figure 1-1: The Kimberley Triangle - study area. Different management strategies are practised on different soil types, but bush encroachment is a common phenomenon in the area.

Scale: 1:300 000

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Objectives

The objectives of this study were to:

- Determine on a broad scale, the current state of plant communities in the study area;
- Relate the state of the plant communities to the measured soil variables and current grazing strategies;
- Determine the relationships, if any, between the presence and level of bush encroachment and the measured soil variables and grazing strategies;
- Determine the long term trends of bush encroachment in a selected section of the study area, making use of aerial photograph analyses;
- Relate these trends, if any, to soil variables and grazing strategies; and
- Draw up guidelines for use by the landowners in the area to assist in the sustainable management of the resource and to possibly control the bush encroachment problem.

5. Thesis layout and structure

This thesis follows the following structure: *Chapter 1* introduces the state of land-use, land degradation and bush encroachment in savanna ecosystems and the implications this holds for various interested parties. Furthermore, the study area, rationale and objectives of the study are discussed. *Chapter 2* is an extensive review of literature on the effects of soil type and grazing on savanna structure and processes, with specific focus on the effects of these on bush encroachment in savannas. *Chapters 3* and *4* are the chapters containing the results of this study. *Chapter 3* focuses on the effects of specific soil variables, and the three management strategies in the study area (cattle, game or communal grazing/browsing), on species composition and distribution in the study area in general. In *Chapter 4* we investigate the dynamics of woody species, and specifically of *Acacia mellifera* (the encroaching species in the study area), from 1957 up to 1993, with the aid of aerial photograph analyses. As in Chapter 3, the aim is to relate observed trends to certain soil variables and the three management strategies mentioned above. These two chapters are written in the format of

journal articles, authored jointly by my supervisor, and will subsequently, with a few minor alterations, be submitted to scientific journals for possible publication. This will explain the use of the plural pronoun throughout the thesis and the positioning of references at the end of each chapter, and not at the end of the thesis. The fact that these two chapters will be submitted to different scientific journals, accounts for the slight differences in format used in Chapters 3 and 4. In *Chapter 5* we attempt to use the knowledge gained from the previous chapters to draw up management guidelines for the sustainable management of semi-arid savannas in general, and also specifically for the interested parties of the Kimberley Triangle Forum.

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Chapter 2

Literature review: Grazing and soil type as factors influencing savanna structure and function

1. Introduction

Savannas are one of the world's most extensive biomes and constitute the dominant vegetation type of Africa (Scholes 1997). They are highly dynamic on all temporal and spatial scales (Vetaas 1992) and occur under a wide range of moisture conditions from humid to arid, and soil conditions, from light to heavy-textured soils (Solbrig 1996; Williams et al. 1996). The term "savanna" refers to those regions of the world, which, in their natural state, have a predominant continuous herbaceous layer, consisting of grasses (usually C_4 species) and sedges (Skarpe 1992) with a woody layer consisting of scattered to numerous trees and shrubs (usually C_3 species). These systems are characterised by a strong seasonality (wet summer/dry winter) with a period of low activity (Solbrig 1996) related to water stress (Van Noordwijk & Ong 1999). Because plant growth is water limited, this term does not include those areas that would develop into woodland in the absence of disturbances such as fire or herbivory (Walker et al. 1981). Semi-arid savannas are those savannas that receive < 400 mm of rain per annum. Soil moisture is one of the main determinants of savanna structure and function, together with soil nutrients, fire and herbivory, the latter two factors acting as modifying agents, influencing the availability of and competition for soil moisture and nutrients (Noy-Meir 1982; O'Connor 1985; Skarpe, 1992; Teague & Smit 1992; Vetaas 1992; Solbrig et al. 1996). These factors interact with each other in complex ways to determine the tree:grass ratio in savanna ecosystems. Knowing the effects and functions of these factors in this ecosystem is important when savanna areas are to be managed on a sustainable basis. Sustainability of savannas is important in South Africa because this savanna biome covers a third of the country (Rutherford & Westfall 1986), and apart from the important contributions of this biome to the informal and subsistence economies, as well as various global and local biological processes (see Chapter 1), it contributes greatly to the formal economy of the country as the main location of the livestock and ecotourism industries (Grossman & Gandar 1989). The usefulness of this important biome is, however, becoming increasingly reduced as large tracts of land become degraded and encroached by woody

species, often thorny *Acacia* species, that leave large areas of land unusable, or with reduced usefulness, for ranching purposes (Grossman & Gandar 1989; Dean & McDonald 1994; Milton & Dean 1995; Hoffman & Ashwell 2001). The carrying capacity of such encroached areas are reduced due to the fact that cattle are grazers, meaning that they do not utilise woody plants, as well as due to the reduced production of palatable grasses and herbs (Ward 2003), and the reduced access to grazing patches through thick, impenetrable, often thorny, thickets that are found in encroached areas (Adams 1967). The relative abundances of the woody and herbaceous layers therefore become increasingly important to land managers, ranchers, and subsistence ranchers.

Here I review the literature on the factors determining the tree:grass ratio in savanna ecosystems, with emphasis on the effects of grazing strategy and soil type on the availability and amounts of water and nutrients in the soil. This will serve as a foundation to the better understanding of savanna dynamics, which will later be used, together with the understanding and insight gained from subsequent chapters, to develop guidelines for the sustainable management of our savanna resources.

2. The determinants of savanna

Models and theories

Over the years, many models have been developed on how savanna systems work, discussing the factors that determine savanna structure and function. One of the early models that include savanna systems, is that of Holdrige (1947). He defined the vegetation formations of the world according to three climate-related parameters, namely temperature, precipitation and evaporation. This model was designed to make broad divisions in the vegetation formations of the world only, and he states that within these divisions local edaphic conditions, such as topography, and disturbances such as alterations by man, will lead to changes in the appearance of the vegetation under similar climatic conditions. Another global model which also describes the environmental conditions that define and limit terrestrial ecosystems, including savannas, is a model by Whittaker (1975). He accentuates climate, specifically rainfall and temperature, as one of the important factors determining savanna biomes, but also recognises the importance of edaphic factors such as topography or soil

conditions, and disturbances such as fire and grazing, in determining the ratio of woody to herbaceous vegetation.

On a local scale, the ratio of the woody to grassy vegetation in semi-arid savannas has frequently been explained by Walter's two-layer hypothesis (Walter 1954; Walter 1971; Walker & Noy-Meir 1982). This hypothesis considers two vegetation components: grasses and trees/shrubs and two soil layers with independent water budgets, except for recharge of water in the deeper layer through the upper layer. Grass roots are restricted to the surface soil, where they are the strongest competitors. Woody species can utilize both soil layers, but are potentially outcompeted by grasses in the surface soil, whereas they have exclusive access to deeper soil resources that carries them through the dry season. Thus, grasses may outcompete woody species in the upper soil layer, and restrict their growth and/or abundance, but generally, woody plants cannot outcompete grasses for water in the upper soil layer (Walter 1954; Walter 1971; Walker & Noy-Meir, 1982; Eagleson & Segarra 1985). If the grass biomass and its competitive ability for soil water is maintained at a low level for a sufficiently long time however, e.g. by several years of intense grazing, then the soil surface changes and water infiltration rate declines, with the result that less water enters the soil but proportionately more of what does enter may penetrate to the subsoil. The result is that woody vegetation may have more water available to it, so the biomass of the existing woody vegetation increases (Walker et al. 1981; Knoop & Walker 1985; Stuart-Hill & Tainton 1989; Skarpe 1990) and the reduced competition in the surface soil layers can lead to *en masse* recruitment of tree seedlings (Ward 2003). These two factors – reduced infiltration and greater biomass of woody vegetation – combine to prevent the re-establishment of grasses even if the grazing pressure is reduced. Only if one or both of these factors are altered to allow the grass to develop to above the critical, unstable equilibrium, will the system revert to its original structure (Walker et al. 1981; Knoop & Walker 1985; Stuart-Hill & Tainton 1989; Skarpe 1990). This hypothesis is regarded by many authors to be an oversimplification of the processes and factors involved in the determination of the structure and function of savanna ecosystems (Knoop & Walker 1985; Kraaij & Ward 2003; Ward 2003). Brown & Archer (1999) noted that encroachment is widespread in areas where only one soil layer exists and Wiegand et al. (2003) also noted this phenomenon in soils too shallow to allow for root niche separation. Walter's (1954) hypothesis, however, still provides a useful theoretical basis to understanding the processes involved in the determination of the

woody:herbaceous ratio in savanna systems. It also forms the basis of many other, more complex models that will be discussed below.

Walker & Noy-Meir (1982) elaborated on Walter's model and demonstrated the existence of dual equilibrium states in such systems as described above, where the soil infiltration capacity declined with reduced grass cover. One state is the tree-grass mixture and the other is a thicket with virtually no grass. Eagleson & Segarra (1985) describe the existence of an opposite situation to the woody/no grass situation, when woodland/mixed savanna changes to grassland. This has often been attributed to excessive killing of trees by elephants, although fire and other herbivores also contribute to the reduction of regeneration rates of trees, increasing tree mortality (Buechner & Dawkins 1961). Pellew (1983) and Norton-Griffiths (1979) suggested that this transition from woodland to grassland is part of a natural large-scale oscillation, as is the transition from the grassland to woody states. McNaughton (1992), however, considers savanna systems sufficiently damped against all but extraordinary disturbances.

Further research lead to the development of models including both plant available moisture and available nutrients. Walker (1987) developed a multi-factor model that incorporated all important environmental factors influencing the vegetation structure of savanna systems. This model shows the complexity of the ways in which environmental factors interact to determine savanna structure and function (Belsky 1990). Later, Solbrig et al. (1996) also predicted the function of savannas in terms of all four determinants of savanna, namely, water, nutrients, fire and herbivory. In addition to water availability as in Walter's two-layer hypothesis, nutrient supply can also modify the vegetation. For a given rainfall zone, vegetation types can be modified by nutrients, so that, for example, a combination of low rainfall and high nutrients (e.g. the Serengeti in Kenya) can support a savanna grassland rather than desert, but a decrease in nutrient supply would be expected to induce desertification without a change in the rainfall. According to this model, soil type, topography, fire and herbivory modify the productivity and rates of water and nutrient flow through the system, determining its structure and function (Van Noordwijk & Ong 1999).

Equilibrium or disequilibrium theories?

Classical equilibrium models, used to explain long-term tree-grass coexistence in savanna systems, have been challenged for arid and semi-arid systems in which rainfall variability appears to be the dominant determinant of system dynamics (Westoby et al. 1989; Behnke & Scoones 1993; Scholes & Archer 1997). These equilibrium models include Walter's (1954, 1971) two layer hypothesis and the Walker & Noy-Meir (1982) model based on Walter's (1954) model (as described above), and have been criticised for two reasons. Firstly, Jeltsch et al. (1996) states that stable tree-grass coexistence may only exist under very specific conditions, for example, where grasses are favoured by water retention in the upper soil layers, as would occur on fine textured soils (Noy-Meir & Walker 1986), and the idea of rooting niche separation is therefore limited in its applicability. In addition, the existence of rooting niche separation under field conditions is questioned (Scholes & Walker 1993; Belsky 1994). Secondly, the applicability of these models, which assume spatial homogeneity in systems characterised by non-homogenous vegetation structure, has been criticised (Jeltsch et al. 2000).

Several alternative models based on a non-equilibrium view have been developed to explain the tree-grass coexistence in savannas. The non-equilibrium view, as presented by Scholes & Walker (1993), states that savannas may not represent a stable mixture of trees and grasses, but an inherently unstable mixture which persists owning to disturbances like fire, herbivory, and fluctuating rainfall. They suggest that disturbance factors such as wind, fire, herbivory and drought, may cause episodic mortality of mature trees, preventing trees from reaching the upper limit of density as determined by inter-tree competition, thus maintaining tree-grass coexistence in savannas. In correspondence with this view, is the idea of savannas as patch-dynamic systems composed of patches of vegetation in disequilibrium within the system (Skarpe 1992; Scholes & Archer 1997; Illius & O'Connor 1999). Patches of almost pure grassland, patches of parkland, or patches of woodland, with patches of intermediary stages will exist due to edaphic, or climatic disturbances, as well as due to variability in factors such as soil properties, herbivory, rainfall, or fire. It has been suggested that on a sufficiently small scale in space or time, all ecosystems will be unstable and transient (Watt 1947), and if perceived from a large enough scale, or over the long-term, these unstable and transient patches together form a dynamic equilibrium (DeAngelis & Waterhouse 1987;

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Ellis & Swift 1988). Savannas can therefore be stable and persistent at a landscape scale, because of the smaller patches within this landscape occurring in different states of transition between grassy and woody dominance (Scholes & Archer 1997).

Scholes & Walker (1993) also proposed a 'multi-dimensional asymmetric' model in which competitive interactions between trees and grasses are asymmetrical and in the favour of trees. They therefore suggest that the tree-grass mixture is not in a competitive balance, as suggested by equilibrium models, but inherently tends to become woodier, but that this state is prevented by disturbance (grazing, fire, drought). Results from a model by Jeltsch et al. (1997) suggest that encroachment in savannas exhibits a threshold behaviour. Above a certain threshold-level of grazing, encroachment will occur, and gradual reversible changes can only occur when stocking rate is below a certain threshold. This limit can be defined as a state within the state-and-transition model where certain states exist within the system which can change into a different state when this threshold level of a disturbance factor, occurs (Westoby et al. 1989). In opposition to this is the suggestion that changes from grassland with scattered trees to woodlands, as would occur in the case of bush encroachment, are linear and irreversible in nature and not cyclical at all as the model of Jeltsch et al. (1997) suggests (Archer et al. 1988).

There seems to be consensus that many interacting factors, operating at various spatial and temporal scales contribute to creating and maintaining savanna physiognomy (Rebertus & Burns 1997). Scholes & Archer (1997) are, however, probably correct to conclude that tree-grass interactions in savanna cannot be predicted by a simple model and ultimately, all assessments of stability and equilibrium may prove to be artefacts of the observed scale (Connell & Sousa 1983; DeAngelis & Waterhouse 1987).

Rainfall

It can be said that soil moisture in particular, as a function of rainfall, and soil nutrients, acts as a determinant in regulating the relative abundance of the woody and herbaceous layers in savanna, while fire and herbivory act as modifiers of the availability of and competition for the first two factors (Vetaas 1992). Many authors have shown rainfall to be the major driving force of vegetation dynamics in the more arid regions (Ellis & Swift 1988; Tapson 1993; Sullivan 1996; Ward et al. 1999). The drier a savanna gets, the lower the biomass and the

metabolic activity, making it relatively weakly interactive so that the dynamics of the system are more event driven. Changes in constraints, particularly rainfall, can then cause step-wise, unpredictable changes in the vegetation (Skarpe 1992) and, in these cases, factors such as herbivory or fire may have comparatively little influence on system dynamics (Ellis & Swift 1988; Skarpe 1992; Behnke & Scoones 1993; Ellis et al. 1993; Sullivan 1996). To illustrate this point, some authors have shown that periods of elevated rainfall may trigger episodes of seed production and seedling establishment of woody plants in grasslands (Turner 1990; Harrington 1991), while drought may promote grass die-off (O'Connor 1993), but have little effect on tree or shrub persistence (Carter 1964). Higgins et al. (2000) developed a disturbance model of tree-grass coexistence in savanna and they hypothesise that this coexistence is driven by the limited opportunities for tree recruitment caused by reductions in grass crop and therefore, fire intensity. They do, however, predict that rainfall-driven variation in recruitment is more important in the drier savannas where fires are less intense and less frequent. Specifically, though, it is not always clear how rainfall variability might constrain, accentuate, or mitigate grazing influences on woody plant emergence and establishment in grasslands (Brown & Archer 1999). Illius & O'Connor (2000) have, however, developed a model applicable to semi-arid grazing systems which would be non-equilibrial if livestock populations are dominated by density-independent drought mortality and are only weakly coupled to vegetation resources. This model tested the hypothesis that such semi-arid grazing systems, prone to climatic variability, might actually be more at risk of extreme herbivore impacts, because droughts may impose more intense and localised defoliation on vegetation than would occur in a system at or near equilibrium. This is because climatic variability causes annual variation in primary production and fluctuations in animal population size, increasing the range of annual defoliation intensities, and producing periods of intense defoliation. They state that this, and the seasonal spatial localisation of herbivore impacts in patchy systems due to animal ranging behaviour, and selective grazing at the level of plant species and patches, makes these systems more and not less prone to ecological change. It is worth remembering though, that the inherent variability in rainfall and soil nutrients found in more arid areas has in the past frequently masked the relatively smaller impacts of grazing on vegetation (O'Connor 1985; Foran et al. 1986; Venter 1989; Milchunas et al. 1989; Parsons et al. 1997; Ward et al. 1998).

Tree-grass and tree-tree interactions

The interactions between herbaceous and woody components are also a factor that influences the structure and function of savanna systems. Although competition for soil water between the grassy and woody components is an essential element of many savanna models (Walter 1971; Walker et al. 1981; Walker & Noy-Meir 1982; Walker 1987) the reported effects of the trees on the grass layer are conflicting. Some authors report lower productivity of the grass layer under tree canopies than in nearby open grasslands (Grunow et al. 1980; Walker & Noy-Meir 1982; Stuart-Hill & Tainton 1988, 1989), whereas other authors reported increased grass productivity under tree canopies (Radwanski & Wickens 1967; Tiedeman & Klemendson 1977; Kellmann 1979; Bernhard-Reversat 1982). Additional increases in woody plant density beyond a critical level, as might be found under bush encroached conditions, may further result in suppression of herbaceous plants, mainly due to severe competition for available soil water (O'Connor 1991; Smit & Rethman 1998, 1999; Richter et al. 2001).

Trees significantly influence the micro-climate under their canopies, thus influencing vegetation structure and composition (Belsky et al. 1989). They intercept direct solar radiation (Belsky et al. 1989, 1993a) which can lower soil temperature and evapotranspiration, increasing soil moisture content (Belsky et al. 1989; Vetaas 1992), although interception of rainfall by through-flow and stem-flow may counteract this effect (Vetaas 1992). Shading also changes vegetation composition by reducing the survival of plants typical to open habitats and improving the survival of shade-tolerant species (Smith & Goodman 1986).

Furthermore, tree litter in the sub-canopy zone alters the physical soil properties and can reduce the soil temperature and evaporation, and improve infiltration, increasing soil moisture content (Tiedemann & Klemmedson 1977). The soil water content of sub-canopy soil layers can also be improved by hydraulic-lift when water absorbed by deep roots from moist soil layers, is transported to, and lost from roots into the drier, upper soil layers (Richards & Caldwell 1987). The nutrient status of sub-canopy soils in semi-arid environments have also been shown by various authors to be improved with respect to the soils between trees (Tiedemann & Klemmedson 1973; Bernhard-Reversat 1982;

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Belsky et al. 1989). Organic matter, nitrogen, phosphorus and soil microbial biomass levels have all been shown to be higher under trees than between them (Belsky et al. 1989, 1993a, b; Belsky 1994; Smit & Swart 1994; Jarvel & O'Connor 2000). This nutrient enrichment of soils under tree canopies can be explained by the fact that trees take up nutrients from surrounding soils and transport and incorporate them into foliage and stem materials that are later incorporated into the soil as litter-fall (Belsky et al. 1989; Scholes 1990; Belsky et al. 1993b; Belsky 1994). Additionally, under-storey plants and associated symbiotic micro-organisms, as well as birds, and grazing and browsing animals attracted to the shade, browse and shelter of the trees all contribute to nutrient enrichment through the decomposition of various excreta (Bernhard-Reversat 1982; Tiedemann & Klemmedson 1973; Belsky et al. 1989; Dean et al. 1999).

The presence of scattered trees within savannas increases the structural heterogeneity of the system and the nutrient enriched patches beneath their canopies support a distinctive, often vertebrate dispersed vegetation (Belsky et al. 1989; Jeltsch et al. 1996). However, the function of trees in savannas varies with their population structure, density and distribution (Jeltsch et al. 1996).

Competitive interactions between trees have also been suggested to play an active role in the spacing of specifically *Acacia*, but also some other species, in savanna systems (Smith & Walker 1983). These interactions are a function of tree size and distance to the nearest neighbour, competition increasing as tree size increases and distance decreases (Smith & Walker 1983). Jeltsch et al. (1996) developed a model to investigate tree spacing and co-existence in semi-arid savannas, and suggests that intra- and inter-specific competition is probably not the factor causing the scattered distribution of trees typical of many semi-arid savannas. They suggest that this distribution is determined by other factors e.g. small-scale heterogeneities in grass density, soil water or nutrient distribution, giving trees in certain localities a better chance for establishment and survival.

Clumped distributions in the tree layer of savannas, as often found in encroached conditions (Skarpe 1991), also occur and might be attributed to intraspecific competition for soil moisture (Skarpe 1991) and/or facilitation (Archer et al. 1988). Aggregated trees protect one another and new recruits under their canopies from fire because these trees suppress

herbaceous production as discussed earlier, resulting in lower fuel loads and less frequent or intense fires (Jarvel & O'Connor 2000).

3. The effects of herbivory and soil type on savanna structure and function

The effects of herbivory on savanna structure and function

Grazing

Natural vegetation in the drier parts of Africa probably evolved under light utilization by shifting populations of indigenous herbivores (McNaughton 1985; Solbrig et al. 1996). Plants in the savanna biome are generally accepted to be adapted to grazing and show a high capacity to recover after grazing events (Milchunas & Lauenroth 1993). Even so, grazing can still have a significant effect on individual plants and plant communities, and on the competitive interactions for water and nutrients within the system. Grazing also directly influences the amounts and availability of these two determinants of savanna structure and function, as discussed below. (Note: For this study the term 'light utilisation' is used as a general term which describes animal numbers, types of animals, season/length of utilisation etc. that does not cause degradation of vegetation in a specific area).

Effects of grazing on savanna plants and plant communities

The grazing optimisation hypothesis (McNaughton 1979; Hilbert et al. 1981; Dyer et al. 1986) states that primary production, or even plant fitness, can increase with grazing intensity and reach a maximum at a moderate rate of herbivory. Such benefits of herbivory to plants have, however, been extensively debated in the past (Stenseth 1978; Owen 1980; Herrera 1982; Choudhury 1984; Lam & Dudgeon 1985; Belsky 1986). For reviews on the literature of the hypothesis that plant consumption may benefit the affected plant, see: McNaughton 1979, 1983; Hilbert et al. 1981; Owen & Wiegert 1981. Belsky (1986) also contributed to this debate and in an extensive review on this subject, discussed evidence provided in support of, and in disagreement with this hypothesis, and concluded that a lack of evidence exists to support the claims that grazing benefits plants. Apart from the debated increase in primary production and short-term fitness under moderate levels of utilisation, though, it has also been shown that moderate levels of grazing may increase species diversity in an area by lowering competition when dominant species are grazed (Naveh & Whittaker 1979; Waser & Price

1981; Noy-Meir et al. 1989). Sustained heavy grazing, on the other hand, can have serious detrimental effects on individual plants and plant communities (Waser & Price 1981; Noy-Meir et al. 1989; Olsvig-Whittaker et al. 1993; Todd & Hofmann 1999).

An individual plant's reactions to grazing depend on the ability of the individual to compensate for a loss of organs and the relative impact of the removal on the competitive relationships in the system in general and specifically in semi-arid savanna grazing systems (Walker et al. 1981). Hence, the particular balance achieved between the perennial and annual or palatable and unpalatable grasses in these systems is the result of the shifting dynamics of competition between them under different levels of utilisation. Grass species differ in their resistance to grazing and therefore their competitiveness under different levels of utilisation. A number of grasses, including many early successional species, can withstand intense grazing because a significant proportion of their biomass is underground (Walker et al. 1981; Fynn & O'Connor 2000). In addition, some grasses develop a recumbent habit when grazed, thereby reducing subsequent grazing, and others are unpalatable or of low food value which protects them from being grazed (McNaughton 1983; Belsky 1992). At the other end of the spectrum are the palatable leafy perennials, regarded as desirable by range managers (Walker et al. 1981; Fynn & O'Connor 2000). These grasses, which are more productive, are also more sensitive to grazing because they lack the underground refuge or recumbent habit and are usually the first to be grazed (Walker et al. 1981). Under intensive or very selective utilisation, the vigour of these grazed species is reduced by the continual depletion of leaf area of grass tufts, and a constant removal of storage products from the roots necessary for the initial flush and growth in the following season (Gibson 1988). Often, under heavy utilisation, the resistant grasses - usually annual, unpalatable species (Waser & Price 1981; Noy-Meir et al. 1989; Olsvig-Whittaker et al. 1993; Todd & Hofmann 1999), and also toxic and spinescent, or woody plants and shrubs (Westoby et al. 1989; Milton & Hoffman 1994) are favoured, and can lead to decreases in species diversity and, in some cases, bush encroachment. Long-term grazing leads to reduced vigour of the grazed species, which makes intensively-grazed perennial grasses poor competitors in general relative to annual grasses that then tend to increase in such ranges (McNaughton 1985).

Intermediate levels of grazing may, on the other hand, prevent the accumulation of dead biomass, which can hinder seedling establishment and germination, lowering diversity and

vigour (Gough & Grace 1998). It has often been found that during periods of low/moderate grazing, the sensitive grasses (palatable or perennial species) are favoured due to the stimulative effect of moderate grazing on individual plants, increasing their competitiveness relative to ungrazed species (Walker et al. 1981; Gibson 1988). Complete removal of herbivores and grazing is also not desirable and may lead to a decrease in species diversity due to competitive exclusion of less competitive species by dominant ones, and might even result in a loss of valuable grazing species from an area (Belsky 1986). In areas where more annual grasses are dominant and underutilisation occurs, litter cover tends to build up because these species are relatively weak in structure as compared to perennial grasses with their strong fibrous structure, and leads to litter formation because they are easily blown over by wind and washed away by rain (Kelly & Walker 1976). In general, in unutilised or underutilised areas, the grass sward becomes moribund, due to the lack of the stimulative effect of grazing, reducing productivity of the grazing land (Walker et al. 1981).

Many studies have shown that intensity of grazing is not the only important factor influencing the species composition of an area. Tainton (1991) and Smit & Rethman (1992) agree that the combination of grazing season, period of occupation, period of rest and stocking density have a greater effect on the vegetation of an area than any of these factors alone. Extended periods of grazing during the growing or flowering season prevent grazed species from recovering after grazing damage and influences reproduction and/or dispersal, which is often more detrimental in causing floristic changes than the same, or higher, intensity of grazing for a shorter period during this season (Tainton & Booysen 1964; O'Connor & Pickett 1992).

Effects of grazing on soil water budgets

Because heavy grazing reduces plant cover in the form of herbaceous vegetation and litter cover, through the removal of plants and plant parts and the replacement of perennial grasses by annual grasses with lower basal cover, there is an increase in the amount of bare soil surface in overgrazed areas (Johnston et al. 1971; Schlesinger et al. 1990). These bare patches are poorly protected from the sun, wind and rain, and experience physical changes in soil properties, i.e. soil compaction and sealing of soil pores (Tromble 1976; Bradford et al. 1988). These soils have a reduced water infiltration capacity due to soil compaction and capping, and lower water-holding capacities due to lower levels of cover which increases evaporation of soil moisture. The changes in species composition from perennial to annual grasses that often accompany heavy grazing, also influence the moisture

budgets of the soil. Apart from the higher cover of perennial grasses which protects the soil from excessive evaporation of soil moisture, these species also capture rainwater in their foliage and funnel it into their rhizopheres, and their absence therefore further reduces water-infiltration (Schlesinger et al. 1990; Skarpe 1992). See Walter's (1954) two-layer hypothesis as discussed above, for the possible consequences of these processes in savanna systems. Heavy grazing further reduces the amount of litter which decomposes to become soil organic matter, which also influences the moisture retention capacity of the soil (Abril & Bucher 1999). Furthermore, it has been found that soil temperature was more extreme under heavy grazing intensities, due to the extreme reductions in plant cover, and this also influences the growth of remaining species, as well as the species that will colonize an area after heavy grazing (Johnston et al. 1971), because plants have an optimal temperature at which metabolic processes take place. All the above factors mean that heavy grazing and the associated reduction in a soil's water-infiltration and -holding capacities, either due to reduced levels of cover, organic matter or physical changes in soil structure, lead to a reduction of the soil's ability to buffer against water stress during the dry season (Abril & Bucher 1999). There is also a general reduction in the resilience of the system, i.e. in the ability of the system to recover from disturbances like fire and grazing which is an integral part of savanna systems, and this can lead to greater opportunities for changes in the tree:grass ratio and also bush encroachment (Pickup et al. 1998).

Effects of grazing on nutrient cycling in the system

In general, the more arid savannas tend to have fertile, nutrient-rich soils (Scholes & Walker 1993). This is because of the lower rainfall in these areas, subjecting the soils to reduced leaching of nutrients (Scholes & Walker 1993). Within these dry, relatively fertile savannas, there exist extensive areas of infertile soils: nutrient distribution within nutrient-rich (or poor) soils can be very patchy (Scholes 1990; Scholes & Walker 1993). The most important nutrients or elements required for plant growth are the macro-nutrients nitrogen, sulphur, phosphorus, calcium, magnesium, potassium, sodium as well as carbon, hydrogen and oxygen, with micro nutrient traces of iron, boron, molybdenum, zinc, copper, manganese and chloride (Campbell 1978; Whitehead 2000). Leguminous plants, which make up a large proportion of southern African savanna vegetation and which rely directly on N_2-fixation for their nitrogen supply (Scholes & Walker 1993), also require cobalt as a nutrient for their rhizobial bacteria (Whitehead 2000).

Of the above-mentioned macro-nutrients, calcium, magnesium, sodium and potassium are not generally thought to be limiting in semi-arid savannas (Scholes & Walker 1993). Nitrogen, on the other hand, is in general the most important nutrient determining herbaceous composition and production (Grunow et al. 1970; Walker & Knoop 1987; Belsky et al. 1993a), and also the most limiting nutrient to plant growth (Russel 1961; Date 1973). In addition, phosphorus has also been shown to be a limiting nutrient in some semi-arid savannas (Tolsma et al. 1987) and specifically in the Northern Cape semi-arid savanna (Donaldson & Kelk 1970). Limitations in herbaceous composition and production in savannas will therefore be determined by the nutrient (N or P) present in lowest relative amount, according to Liebig's law of the minimum (Miller & Gardiner 1998). These two nutrients are of further importance in the determination of savanna structure and function because deficiencies limit non-N_2-fixing grasses more than N_2-fixing *Acacia* species and P has also been shown to be a major limitation in plant and, specifically, grass production when shortages exist in the soil (Donaldson & Kelk 1970; Oberson et al. 1999). Under rangeland conditions, however, these nutrients and elements are continuously removed from the soil via the meat products that are harvested, leading to a net efflux, making the soil that remains deficient in certain or all of these elements (Campbell 1978).

Nutrients in savanna grazing systems are consumed as part of the grazed plant by the grazing animal, excreted and returned to the soil through the death and decomposition of plant and animal residues. In addition there may be nutrient inputs from the atmosphere or through fertilisers, and losses from leaching or volatilisation from the soil (Whitehead 2000). In general, large herbivores speed up the nutrient turnover rate in savannas (Ruess & McNaughton 1987; Whitehead 2000). Only a small proportion of any of the nutrients consumed are utilised by the grazer and the rest are returned to the soil through dung in mainly insoluble form, and urine, in water soluble, plant-available form (Whitehead 2000). Despite the immediate availability of nutrients, and especially nitrogen, to plants in the urine of grazing animals, it has been suggested by several authors (Denmead et al. 1974; Ryden et al. 1984) that herbivores are a major pathway of nitrogen losses in grasslands. Urine is a concentrated solution, deposited on a small area, and urine patches are likely to contain nitrogen in excess of plant demand. Under such conditions, the retention of nitrogen in the soil system might be reduced, with losses from the system occurring through various processes such as leaching, denitrification, and ammonia volatilisation. Conclusions from studies on the net effect of this type of nutrient cycling are, however, contradictory

(De Mazancourt et al. 1999). It is, however, generally accepted that heavy grazing leads to increased removal of nutrients from the system in animal production or through an increase in the unavailability of those nutrients that are excreted in dung. Kraaij & Ward (2003) have conducted field and pot experiments on the factors causing bush encroachment by *A. mellifera* in a semi-arid savanna north of Kimberley, Northern Cape, since 2000. They focused on the effects of rainfall, grazing, fire and nitrogen addition on the germination and survival of this species. They found, among other things, that while rainfall increased germination and survival of this species, the addition of nitrogen led to a decrease in germination and survival, suggesting that losses of nitrogen from the system, as would occur under heavy grazing conditions, might favour woody growth more than it does grassy growth, and this might provide opportunities for bush encroachment. This again illustrates the importance of water and nutrients in the determination of savanna vegetation dynamics.

Nutrient redistribution in savanna soils through the dung and urine of grazing animals further leads to spatial variability in soil nutrient status and has been found to be most marked with nitrogen and potassium (Whitehead 2000). This patchy distribution and large spatial variation in the nutrient status of the underlying soil, often leads to patchy plant distribution (Weber et al. 1998). This effect is also seen on a larger scale because of the tendency of animals to excrete in certain areas e.g. around water points or under shady trees, concentrating nutrients in these areas (McNaughton 1983; Belsky et al. 1989; Whitehead 2000). This may increase soil fertility beneath tree canopies for long periods (Vetaas 1992) and can even change the species composition in these areas significantly from the surrounding non-enriched areas (Belsky et al. 1989).

Apart from the removal of nutrients from the system in animal products, very high levels of grazing removes nutrients from the system through high levels of litter consumption by the grazing animal (Abril & Bucher 1999; Whitehead 2000). In semi-arid grasslands, plants derive their nutrients almost entirely from recycling processes, mainly the death and decay of plant material, with only small inputs from the atmosphere and the weathering of soil minerals (Whitehead 2000). Removal of litter by cattle effectively deprives soils of nutrients coming from litter decomposition (Abril & Bucher 1999) especially nitrogen, phosphorus and/or potassium (Whitehead 2000). High levels of litter consumption furthermore lead to reduced soil organic matter content. This not only leads to reduced water-holding capacity of the soil, as discussed above, but also to reduced nutrient-holding capacity and therefore

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nutrient content, especially soil nitrogen, than would otherwise have been experienced (Abril & Bucher 1999; Schlesinger et al. 1990). Heavy grazing therefore leads to a general decrease in soil nutrient content and this may favour N_2-fixing species more than non-N_2-fixers, leading to encroachment (Johnston et al. 1971; van Auken & Bush 1989; Abril & Bucher 1999).

At the other extreme, underutilization is also not necessarily beneficial. When large herbivores are removed, the high amounts of standing biomass will lead to loss of nutrients from the system due to fire (Skarpe 1992) and, additionally, a rapid loss of nutrients from the surface soils to deeper soil layers can occur, making it available to trees and shrubs with access to nutrients and moisture in the deeper soil layers. This may, in some cases, lead to an increase in woody growth (Skarpe 1992; Abril & Bucher 1999). Moderate degrees of grazing, on the other hand, concentrate the nutrient flux at the soil-plant-herbivore interface, reducing leakage of nutrients to deeper soil layers and keeping the nutrients in circulation and available for use mainly by the herbaceous layer (Skarpe 1992).

Effects of grazing on fire regime

Intense fires usually kill the aerial tissue of savanna shrubs, most of which subsequently coppice from the base (Trollope, 1984; Bond & van Wilgen 1996; Gignoux et al. 1997). Woody meristems within the flame zone (< 5 m), are generally more exposed to fire damage than grass meristems and the latter can recover more efficiently in the short term (Trollope 1974). Frequent fires therefore benefit grasses and suppress the recruitment of mature woody plants (Roques et al. 2001). Grazing, however, reduces the standing crop of grasses and thus fire frequency and intensity (Norton-Griffiths 1979). In this way, fire-control of the establishment of woody vegetation is reduced. This is an important reason for establishment of woody species in heavily-grazed savanna ranges (Noy-Meir et al. 1989; Skarpe 1992; Milton & Dean 1995; Roques et al. 2001).

Effects of grazing on encroachment

A variety of direct and indirect effects of livestock grazing may interact to promote woody plant seedling establishment in grass or open savanna communities, leading to bush encroachment. For woody plants that are dominant or exclusive seed propagators, with potentially long life spans and low post-establishment mortality rates, seedling recruitment is probably the most critical stage in their life-history (Harper 1977) although many woody

species and also encroaching woody species, are clonal species or resprouters too (Scholes 1997). Changes in species composition and reductions in herbaceous plant basal area, density and above and below ground biomass (i.e. reduced herbaceous plant competition) known to accompany chronic livestock grazing might create opportunities for tree and shrub seedling establishment in savanna grasslands (Brown & Archer 1999). Some studies support this hypothesis (Schultz et al. 1955; Smit & Rethman 1992; McPherson 1993; Bush & van Auken 1995) but others do not (Brown & Archer 1989; Schmidt & Stubbendieck 1993; O'Connor 1995). The fact that many encroached areas are heavily grazed cannot be taken to mean that heavy grazing and its effects on the competitive interactions in savanna systems, causes this state (Ward 2003). Indeed, Brown & Archer (1999) noted that bush encroachment occur widely in areas with light or infrequent grazing. Johnston et al. (1971) found some species that are not usually encroaching, to encroach in grasslands in lightly and moderately grazed areas, but found that encroachment was prevented by browsing and trampling in heavily and very heavily grazed areas, showing that under-utilization can also have disadvantages when a tree:grass ratio optimal for livestock ranching is the aim. Some authors have suggested that the response of woody vegetation to grazing utilization is non-linear in nature and that a threshold level of utilization intensity above which grazing will result in high shrub cover, exists (Skarpe 1990; Jeltsch et al. 1997; Weber et al. 2000, Ward et al. 2000). This threshold differs regionally depending on the type and state of the vegetation. Weber et al. (1998), (2000) modelled long-term vegetation responses to alternative stocking strategies, and concluded that grazing heterogeneity, or selectivity of livestock in both quantity and quality of forage, is very important in the determination of this grazing threshold (Weber et al. 1998). This effect of grazing heterogeneity is due to the fact that this leads to increased heterogeneity in soil resources, which would promote increases in shrub cover in semi-arid rangelands (Weber et al. 1998). Furthermore, heterogeneous grazing will favour shrub colonisation due to the larger frequency of heavily grazed sites open for shrub colonisation. Consequently, in ranges prone to shrub cover increase, low grazing heterogeneity is desirable (Owens et al. 1991).

Browsing

Although primary production in savannas is distributed equally between the herbaceous and woody plant components, in the past, commercial animal production in the savanna regions of South Africa was based almost entirely on a single species of bulk grazer, namely cattle (Owen-Smith & Cooper 1985). The absence of browsers in the system has in some cases been associated with encroachment (Roques et al. 2001). Stuart-Hill & Tainton (1988) found that, in the short-term, browsing had a stimulative effect on tree vigour, increasing their competitiveness for water and nutrients, resulting in a lowered grass yield under trees. In the long term though, frequent intensive browsing may reduce the vigour of the tree, especially when browsing occurs during immature stages of tree growth (Stuart-Hill & Tainton 1988; Bryant et al. 1983). High browsing pressure can therefore retard the growth of trees and shrubs (Pellew 1983) and in this way prevent the propagation and establishment of woody plants (Prins & van der Jeugd 1993). Furthermore, retardation of the growth of shrubs prolongs the exposure of shrubs to fire and suppresses recruitment into the mature stages. Roques et al. (2001), found that moderate levels of browsing was not closely related to change in cover of woody vegetation, but its absence was typically associated with encroachment, while very high values were associated with declines in cover. On the other hand, the browsing of seed pods and subsequent dissemination of the seed in dung can have a positive influence on shrub recruitment (Brown & Archer 1987), although the seeds of *A. mellifera,* an important encroacher in the Northern Cape, South Africa, are probably killed when ingested by ruminants due to its thin seed coat (Dave Joubert, *pers. comm.**).

The effects of soil type on savanna structure and function

In general, at the landscape scale, close relationships exist between species-level vegetation composition and soil in savanna systems (O'Connor 1992; Scholes & Walker 1993). On a global basis, it has been said that the height and spacing of the woody and grassy components of savanna vegetation is influenced greatly by soil moisture conditions, while the species composition varies with soil nutrient status (Cole 1982). The

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broad-scale distribution of the main structural and floristic vegetation types in southern African savannas is indeed highly predictable from knowledge of the water and nutrient availability of the environment which is mainly determined by soil type (Medina & Silva 1990). Not surprisingly, savanna vegetation follows changes in certain soil properties so closely that in the semi-arid savannas of Namibia, it has been found that the form and composition of the vegetation are so closely related to the nature and depth of the soil, that the presence of certain sedimentary sequences of rock could be identified by means of the vegetation patterns on satellite images of the area (Cole 1968; Cole & Le Roux 1978).

The effects of soil type on the availability and amounts of water and nutrients for plant growth

In southern African semi-arid savannas, water availability is the factor that determines the period of time in which plants can grow through its effects on the period that primary production and nutrient mineralization can occur (Scholes & Walker 1993; Scholes 1997). Nnutrient availability regulates the rate of growth during this period (Scholes 1997). In these systems aboveground primary production of the herbaceous layer has been known to be linearly related to annual rainfall up to 900 mm. The slope of this relationship between primary production and rainfall is determined by soil fertility and the y-intercept is controlled by tree biomass and soil physical characteristics (Rutherford 1980; Scholes 1993). This illustrates the strong relationship that exists between plant productivity and soil type, which affects soil moisture and nutrient presence and availability. Additionally, Scholes & Walker (1993) ascribe the marked difference between savanna vegetation under the same climate, but on different soils, to the effect of soil texture on the availability of soil moisture, and the effects of soil fertility.

Soil factors affecting water availability and content

Soil structure is influenced by the relative proportions of the sand, silt and clay particles in the soil, as well as by the amounts of organic matter present, (Barber 1984) and these two factors (soil structure and organic matter content), are major determinants of the amount and availability of soil moisture in a given area at any given time (Campbell 1978; Barber 1984; Solbrig 1990). The size of the inorganic soil particles determines the ease with which water passes into and through the soil and the amount of water retained in air-dry soil (Flocker & Nielsen 1962; Barber 1984). Organic matter content of a soil influences water content and availability both through its hydrophylic characteristics and through its positive

effect on soil structure (Campbell 1978; Barber 1984; Knoepp et al. 2000; Reynolds et al. 2002). Gravels and sands have the advantage of water infiltrating easily, due to large pore sizes, but it also evaporates more readily from such soils because of the large air spaces between the soil particles. These coarse-textured soils also have little power of raising capillary water from the ground water below and little power of holding water for extended periods of time because of the often low amounts of organic matter retaining moisture in these soils. Consequently they easily become very dry, unless constantly supplied with water, and soil moisture in these soils is only available for use by plants adapted to survive in such conditions and then only for limited lengths of time (Reynolds et al. 2002). On the other hand, the smaller and denser the soil particles, the lower the infiltration rate of water into the soil, but also the slower the evaporative rate, and fine textured soils tend to take longer to desiccate. At the extreme end however, very fine textured soils, i.e. clays, hold water very strongly due to the tension caused by the immense aggregate surface of the great number of microscopic, plate shaped, soil particles. This means that a clay soil can hold water so strongly that the plant roots cannot absorb it, experiencing the effects of desiccation although there is more than enough water present in the soil. Because of its high soil bulk density root penetration often becomes limited as the clay content increases (Barber 1984). Organic matter may improve these physical soil conditions by improving the aggregation of soil particles which lowers soil bulk density (Reynolds et al. 2002), thus improving drainage and infiltration and fostering more extensive and deeper plant root systems, which may effectively make more moisture available to vegetation (Campbell 1978). It also increases percolation of water into the soil by holding water on the soil surface long enough for it to enter the soil (Campbell 1978). In addition, it decreases evaporation of moisture from the soil, and organic litter cover also protects the soil against crust formation and thus increases the rate of water infiltration (Campbell 1978).

These effects of soil structure and organic matter content of a soil on savanna vegetation is clearly seen in southern African savannas where parkland vegetation (large, scattered trees in a grass layer) with deep-rooted, woody species, such as *Acacia erioloba*, as the dominant woody species, are largely confined to deep sandy soils (Cole 1982). Although root penetration is not impaired in these soils, soil moisture is relatively scarce, explaining the dominance of those woody species with roots that can reach the water table (Cole 1982). Such species have a competitive advantage over other woody species which are consequently excluded from such areas. As the soil texture becomes finer i.e. loamy soils, woody

vegetation increases because these soils hold enough soil moisture to sustain woody vegetation but are still well drained (Cole 1982). Trees often disappear and shrubs are small and sparsely distributed in clay soils due to its fine texture and poor drainage and grasses and some forbs out-compete woody species in these areas to dominate such soil types (Cole 1982). Scholes & Walker (1993) noted the same relationship between sol texture type and the presence and amount of woody vegetation. They attribute this trend partly to the different hydrological characteristics of the different soils.

Soil factors affecting nutrient availability and content

Soil texture potentially influences the rate at which nutrients, dissolved in the soil solute, are mineralized, transported, and absorbed by plant roots. As soil texture gets finer, there will be a reduction in soil moisture or soil moisture movement, due to lower infiltration and increased resistance to water flow, slowing the movement of soil water and the supply of nutrients that are dissolved in the soil moisture, to the plant root. A lower supply of soil moisture thus leads to a lower supply of nutrients to the plant (Tisdale et al. 1990; Warncke & Barber 1972). In addition to the effect of soil structure on water movement and therefore nutrient availability in a soil, the amount of clay particles in a soil also affects the amount of nutrients through its positive effect on the cation-exchange capacity of a soil (Barber 1984). The cation-exchange capacity determines the quantity of cations that can be adsorbed in an exchangeable fashion in a soil (i.e. not susceptible to leaching but available to plants) (Whitehead 2000). Cation-exchange capacity is usually closely related to soil fertility (Tisdale et al. 1990).

Organic matter, as a factor influencing soil texture, is also very important in nutrient supply, both directly and indirectly. Directly, organic matter provides almost all of the nitrogen and much of the phosphorus and sulphur in grassland and savanna soils (Whitehead 2000). Indirectly, organic matter also contributes to the cation-exchange capacity of a soil and thus plays a major role in supplying nutrients for plant growth (Campbell 1978; Knoepp et al. 2000; Scholes 1990). As a rule, soils with large amounts of clay and organic matter will have higher cation-exchange capacities than sandy soils low in organic matter (Tisdale et al. 1990).

The structure, function and composition of southern African savannas are all highly influenced by nutrient availability, especially that of nitrogen and phosphorus (Scholes 1990; Scholes 1993). Phosphorus, however, only becomes limiting when nitrogen deficiencies are

ameliorated (Liebig's law of the minimum). Under natural conditions plants absorb most of their nitrogen from the soil solution in mineral form and only very small amounts are absorbed as organic substances. Legumes may fix nitrogen from the atmosphere through a symbiosis with *Rhizobium* (Date 1973), and through this relationship are not limited by nitrogen deficiencies. Grasses, on the other hand, do not generally have this ability and in areas where nitrogen are limiting (Chalk 1991), woody vegetation will have the competitive advantage over grasses. This provides the opportunity for woody vegetation to increase and encroach.

Soil pH may limit *Rhizobial* infection of plant roots, thereby influencing the nitrogen fixing ability of, and competitive interactions between N_2-fixing woody species *vs* non-N_2-fixing grasses (Jenkins et al. 1988). Furthermore, soil pH indirectly influences the amounts and availability of nutrients through its effect on biological activity in the soil (Knoepp et al. 2000). Biological activity is higher in nutrient-rich, neutral, or alkaline soils than in nutrient-poor, acid soils (Trudgill 1988). Nutrients contained in plant litter are unavailable for uptake by plant roots until they have been mineralized into an inorganic form. For example, in savannas, organic nitrogen is transformed into ammonium- (NH_4^+) or nitrate- (NO_3^-) ions by micro-organisms before uptake. Without these organisms and processes, effective nitrogen deficiencies would exist in the soil. This holds the possibility of bush encroachment in acid soils with effective nitrogen deficiencies, as described above.

Soil factors affecting the ability of the plant to obtain soil moisture and nutrients

Plant root growth and morphology can be severely influenced by soil structure (Barber 1984; Flocker & Nielsen 1962). Soil structure to a great extent determines the bulk density of a soil and the ease with which roots can penetrate soil in the following ways: The higher the bulk density for a given textural class, the more compact the soil, the more poorly defined the structure and the smaller the amount of pore space. (Tisdale et al. 1990). Apart from the lower levels of oxygen for root respiration (Taylor & Gardner 1963; Reynolds et al. 2002), a high soil bulk density offers more resistance against root penetration and elongation (Tisdale et al. 1990; Flocker & Nielsen 1962; Reynolds et al. 2002; Taylor & Ratliff 1969; Peterson & Barber 1981) and in most cases total plant growth becomes reduced (Oliver & Barber 1966). Dye & Walker (1980) noted that soil factors influencing root penetration i.e. soil structure and depth, significantly influences species composition. They

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found that on deep soils, providing sufficient rooting depth, perennial grasses occurred in abundance and woody vegetation could establish successfully. In sites with shallow soils, vegetation cover, in general, was sparse due to the fact that water and roots can penetrate to a limited depth only, and herbaceous species that occur in these areas are mostly annuals. This implies that increases in woody vegetation would be limited in shallow soils, making such soils less prone to encroachment.

4. Conclusion

It is clear that, despite extensive research, there is still some controversy on the exact nature of the processes involved in the determination of the tree:grass ratio in savannas. Furthermore, the role and effects of modifying factors such as grazing, fire or soil type, in savanna systems, is not quite clear, although important. Generally, it is accepted that grazing acts on savanna structure and function mainly through its effects on the competitive abilities of individual plants within the system. Soil type is more directly involved in determining the amounts and availability of moisture and nutrients and thus affects the tree:grass ratio within savannas. The fact remains, however, that the causes of bush encroachment, a state of high tree:grass ratio in savannas, is not clearly understood, making it difficult to prevent or manage this state. It is even sometimes suggested that once bush encroachment occurs, it is irreversible (Archer et al. 1988). This holds important ramifications for conservationists and land managers in South Africa where much of the country's economy depends on the ecotourism and ranching industries based in savannas. Subsistence farmers too are highly dependent on savanna systems with an acceptable tree:grass ratio for their livelihoods.

Much of the prevailing rhetoric in rangeland science today, focuses on the non-equilibrial nature of rangeland systems and emphasises the inappropriateness of equilibrial-based models for range management (Fernandez-Gimenez & Allen-Diaz 1999). This is also the case with savanna systems. What are the management implications of this shift in rangeland philosophy? Firstly, we must guard against the misapplication of the non-equilibrium approach. In extreme cases this might lead to the notion that grazing intensities, often expressed as stocking rates, are irrelevant in the management of savanna systems in South Africa, which experiences high levels of climatic variability. The literature, as summarised in this chapter, provide countless examples to the contrary. A purely ecological approach to

rangeland management, which often suggests drastic destocking of the natural vegetation, is, however, unrealistic, especially in a country like South Africa where natural resources are put under more and more pressure as the human population increases. If, however, bush encroachment shows a threshold behaviour (Jeltsch et al. 1997), as suggested by some non-equilibrium views, economic production might be increased or maintained for a number of years, without significant degradation of the natural vegetation. In the long-term, the cost of managing bush encroachment might, however, prove too high. An acceptable balance between the ecological and economic approaches, therefore needs to be found (Jeltsch et al. 1997). Continued research in savanna regions to improve our understanding of these systems might help to eventually determine how to achieve this 'acceptable balance'.

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Chapter 3

The effects of soil variables and grazing strategy on species composition in a semi-arid savanna

1. Abstract

The tree:grass ratio of savannas is important, especially in the semi-arid savannas of South Africa where this vegetation type contributes greatly to the livestock and eco-tourism industries. Increases in this ratio leads to reduced productivity and profitability of rangelands. Of the principal factors determining savanna structure and function (soil moisture, nutrients, fire and herbivory), we investigated the effects of soil type, which influences the presence and availability of soil moisture and nutrients, and grazing strategy on the presence and distribution of plant species in the study area through vegetation classification. Heavy livestock grazing is generally believed to lead to increases in the tree:grass ratio, although we found that grazing strategy is not as important as soil type in determining species presence and distribution. We did, however, find that of the grazing strategies studied, communal grazing has the greatest potential to cause general vegetation degradation. Soil texture, through its physical effects on plant growth and its effects on soil moisture and nutrient presence and availability, which in turn affects the competitive relationships between N_2-fixing woody species and non-N_2-fixing grasses, is crucial in the determination of the tree:grass ratio. We suggest that habitats with sandy soils and clay-pan habitats are resistant to bush encroachment by N_2-fixing species due to moisture deficiencies, soil texture and/or heavy utilisation. Heavy utilisation of rocky areas, as well as loam, sand, and clay combination soils, which remove the suppressive competitive effect of grasses on the woody vegetation, may lead to bush encroachment. Hence these areas should be managed conservatively. Because of the importance of soil moisture in limiting woody plant germination and initial survival, we suggest that heavy grazing in above-average rainfall years should be limited in all habitats.

Keywords: Randomisation techniques; canonical correspondence analysis; Braun-Blanquet vegetation classification; bush encroachment; N_2-fixing species; game, cattle, communal grazing; soil texture; soil moisture; soil nutrients.

2. Introduction

The savanna biome covers a third of South Africa (Rutherford & Westfall 1986), with at least 84 % of this land used for extensive ranching purposes, i.e. cattle, game and subsistence ranching (Grossman & Gandar 1989). This biome further contributes greatly to the South African ecotourism and hunting industries (Grossman & Gandar 1989). Because in South Africa this vegetation type is too dry to support agricultural land-use types other than those based on grazing/browsing, the ratio of the herbaceous to woody components in these areas is very important. Increases in woody plant abundance in savannas, with accompanying changes in herbaceous cover and composition (termed bush encroachment - O'Connor & Crow 2000; Hoffman & Ashwell 2001), have, however, been documented worldwide (Harrington & Hodgkinson 1986; Hobbs & Mooney 1986; Johnson et al. 1993; Sholes & Walker 1993; Kreuter et al. 1999; O'Connor & Crow 2000) and also in South Africa (O'Connor 1985; O'Connor & Crow 2000; Kraaij 2002). Areas that are bush encroached have a considerably lower productivity and profitability than non-encroached areas. This is because encroaching species are often unpalatable to livestock because of chemical and physical defences (Rohner & Ward 1997). Bush encroachment also leads to reduced production of palatable grasses (Ward 2003), and access to grazing patches is restricted through the dense, and often thorny, thickets that often form in encroached areas (Adams 1967).

Heavy grazing by livestock, and the replacement of indigenous browsing animals by cattle, are often seen as the primary causes of bush encroachment (Noy-Meir 1982; Skarpe 1990; Ward et al. 2000; Hoffman & Ashwell 2001). This opinion originated from a model by Walter (1954), often referred to as Walter's two-layer hypothesis. In this model, it is proposed that the structure and function of savannas is determined by the competitive interactions between the woody and herbaceous layers for soil moisture. Coexistence of trees and grasses are then proposed to be possible due to rooting niche separation in different soil layers. The hypothesis states that grasses outcompete woody species with regard to water in the upper soil layers, leaving limited amounts to penetrate to the deeper soil layers where it is exclusively available to the woody vegetation. When the grass layer is damaged by e.g. heavy grazing (often by cattle), more water becomes available in the deeper soil layers for woody growth. This provides the opportunity for woody species to increase and for certain

species to encroach. For this same reason, bush encroachment is often believed to predominate in communal/subsistence rangelands, where heavy grazing persists (Walker et al. 1981), and also that the impacts on the environment of these forms of land-use are greater than that experienced in commercially farmed areas (Archer et al. 1989). In addition, browsing by game species is even thought to improve vegetation structure by controlling the establishment and recruitment of woody species in savannas (Trollope 1980; Scholes & Walker 1993). Walter's (1954) two-layer hypothesis is, however, generally regarded as an oversimplification of processes and factors involved in the determination of savanna dynamics and structure (Knoop & Walker 1985; Kraaij & Ward 2003; Ward 2003), and some observations contradict this hypothesis (see Brown & Archer 1999; Wiegand et al. 2003). In addition, recent studies have shown that general land degradation is not always a result of communal pastoralism (Ellis & Swift 1988; Archer et al. 1989; Tapson 1993).

As an alternative to Walter's (1954) two-layer hypothesis and other equilibrium theories, it has been suggested that disturbance factors such as herbivory, fire and climate in the form of extreme and erratic rainfall events, as well as the heterogeneity of the environment, i.e. topography and soil properties, in addition to the direct effects of soil moisture and nutrients, all contribute to determine tree-grass dynamics within savanna systems (Scholes & Walker 1993; Skarpe 1992; Scholes & Archer 1997; Illius & O'Connor 1999). The specific factors determining, and the processes involved in the determination of the tree:grass ratio, and also bush encroachment in savannas, are, however, still not clearly understood (Teague & Smit 1992; Smit et al. 1996; Ward 2003).

In this study, we set out to explore the effects of different management strategies (game, cattle and communal grazing) and soil types, and the interactive effects of these factors, on the presence and distribution of plant species (for example: ratio of woody *vs* herbaceous, palatable *vs* unpalatable species) within a semi-arid savanna in the Northern Cape, South Africa. Semi-arid savannas are arbitrarily classified as those savannas receiving less than 400 mm of rain per annum. We suggest that the three different management strategies (cattle, game or communal herbivory), will affect the environment, and specifically the vegetation dynamics, differently due to differences in stocking rates and herbivore composition (grazer:browser ratio), under each management strategy. We further know that vegetation structure and composition are closely linked to soil type in savannas

(Medina & Silva 1990; O'Connor 1992), differences in plant communities often being due to differences in certain soil characteristics. We suggest that soil characteristics such as those measured in this study, mainly influence vegetation structure and function through thier effects on the amounts and availability of soil moisture and nutrients to the vegetation. The study area, called the Kimberley Triangle, consists of various game and/or cattle ranches, which are owned by private landowners and various organizations. Additionally, a portion of the study area is a State-owned conservation area, and there is a communal piece of land owned and managed by the community of some 150 families that lives there. A shared problem on all of this land, regardless of management strategy, or soil type, is bush encroachment to a greater or lesser degree. Therefore, this study area is ideal for a study investigating the effects of different management strategies on different soil types, on the vegetation dynamics in a semi-arid savanna. This might shed some light on the existing controversies on the effects of different forms of grazing on the tree:grass ratio, and also on the relative impacts of spatial heterogeneities, i.e. soil type, on these processes.

3. Materials and methods

Study site

Physiography, geology, soils, and land types

The Kimberley Triangle, a 100 000 ha block of land, is situated north of Kimberley, Northern Cape, South Africa, and is bounded by the following coordinates: 28° 27' 04'' S, 24° 42' 03'' E and 28° 44' 05'' S, 24° 41' 00'' E. The landscape varies from flat to gently undulating plains and small, andesitic hills. Altitude varies from 1 000 m to 1 250 m above sea level. Shallow undefined drainage channels, all non-perennial, occur over most of the region. This pattern is broken by the occurrence of two steeply sloping, deeply incised strips of land adjacent to the Vaal River to the north and west (Bezuidenhout 1994, 1995).

The largest proportion of the study area is comprised of red and grey aeolian dune sand, with andesite of the Ventersdorp supergroup often occurring next to the Vaal River but also in extensive patches near the southern border of the study area (Geological Survey 1993). Calcrete and surface limestone occurs in patches in the south-eastern and -western corners of

the Kimberley Triangle with an isolated patch in the northern corner. Patches of alluvial diamondiferous gravel and small areas of siltstone, shale, quartzite and gritstone of the Griqualand west sequence, occur in the aeolian sand formations in the northern and north western corners of the study area (Geological Survey 1993). In addition, in the south-western corner of the study area, an isolated patch of a tillite, sandstone, mudstone and shale mix of the Prince Albert formation, Karoo sequence, occurs. In the easternmost corner, patches of shale also of the Prince Albert formation, Karoo sequence, as well as some dolerite intrusions occur (Geological Survey 1993).

Four land types occur in the study area (Anonymous 1987; Bezuidenhout 1994, 1995):

(1) *Ae* - The A unit refers to red-yellow, apedal, freely drained soils, without water tables. The Ae land type refers to red soils with a high base status with a depth of 0,1 to more than 0,3 m.

(2) *Ah* - The Ah land type varies from the Ae land type in that it also includes yellow soil and is consistently deeper than 0,3 m and usually contains less than 15 % clay.

(3) *Fc, Fb* - The F unit refers to land types that usually contains soils from the Glenrosa and, or Mispah forms, although other soils may occur. It further indicates land where the dominant soil-forming processes have been rock weathering, typically giving rise to lithocutanic horizons. The Fc land type occurs in the south western corner of the study area and refers to areas where lime is usually present in the landscape. In the eastern parts of the study area, lime is rare or absent in the upland soils but generally present in low-lying soils (Fb-type) (Anonymous 1987; Bezuidenhout 1994, 1995).

Vegetation

The study area is classified as Kimberley Thorn Bushveld and falls within the savanna biome (Van Rooyen & Bredenkamp 1996). Acocks, a well known botanist who conducted vegetation classifications in South Africa for many years, classified the vegetation in the study area as Kalahari Thornveld invaded by Karoo (veld type 17), while a small section along the banks of the Vaal River, bordering the study area, consists of False Orange River Broken Veld (veld type 40) (Acocks 1975). One of the interesting, conservation-worthy features of the vegetation in the study area is the transition found between two biomes, namely the Savanna Biome and the Nama-Karoo Biome that is found in the southern parts of

the study area (Bezuidenhout 1994, 1995). Species nomenclature follows that of Arnold & De Wet (1993).

Climate

The Kimberley Triangle falls in the summer rainfall area of South Africa. The climate can be described as semi-arid with the long-term mean annual rainfall of Barkly West (the closest town to the study area) being 388 mm. As is often the case in the semi-arid and arid areas, rainfall is extremely variable (C.V. = 39 %) and the 100 year (1892-1992) minimum total rainfall was measured as being 122.7 mm with the 100 year maximum total rainfall 977.6 mm. Precipitation occurs mostly in the form of thunderstorms in the months of January, February, and March, with little rain falling from May to October. The total rainfall for the year in which fieldwork were conducted (January 2001 to January 2002) was 600 mm. The months of November to February experience daily maximum temperatures exceeding 30°C and can be as high as 44°C. For the remainder of the year the days are warm and in winter the nights are cold (coldest months June-July) and frost occurs (Bezuidenhout 1994; Kraaij 2002).

Data collection

Vegetation sampling and analysis

Vegetation classification
The Braun-Blanquet floristic association method for vegetation classification (Mueller-Dombois & Ellenberg 1974), also called the Zürich-Montpellier method (Werger 1974), was used to classify the vegetation communities in the study area. Sampling was done from January 2001 up to January 2002.

Sampling design and layout
Sampling was done on a stratified random basis. Sampling was stratified according to ranch; ranches being representative of grazing strategy on specific soil types. Positioning of sampling plots was done in a way that would make them most representative of the plant community being sampled. This introduced some subjectivity into the sampling design, but

maximised sampling efficiency can be achieved in this way because obviously heterogeneous plots can be avoided as far as possible. This sampling method was preferred over a truly random or systematic sampling design because it tends to take into account the underlying non-random relationships between biota and the physical environment and in this way the sampling of plots that are unrepresentative, or plots that represent a transition between plant communities, can be avoided (Werger 1974; Gillison & Brewer 1985).

The minimum number of plots per ranch was determined by plotting the coefficient of variation in number of plant species per plot (y-axis) against the cumulative number of plots per ranch (x-axis). The asymptote of the resulting curve was determined and the corresponding value on the x-axis was taken to indicate the minimum number of plots needed to sample each ranch representatively. This resulted in a total of 140 relevés in the study area. In order to determine plot size and form, a preliminary field study was conducted in May 2001, in which the nested plot technique and consequent species-area curve, as described by Mueller-Dombois & Ellenberg (1974), was used to determine the minimum size of sampling plots in each major vegetation community type. For the sake of direct comparison among vegetation types, the size of sampling plots in all vegetation community types was positively adjusted to 1 000 m^2. In the Braun-Blanquet method, one is not restricted to a fixed plot form in sampling the vegetation of a region, because species are rated on a cover-abundance scale with relative values (Werger 1974). For logistical reasons, however, the form of the sampling plots was set out as 50 m x 20 m plots in all the vegetation types except for the clay-pans habitat type (see 'Results, section 3.1.' for description of this habitat type), where the plots were set out as 10 m x 100 m plots, to take the stratification of the vegetation within the pan into account.

For the purposes of this study, the cover-abundance scale usually used with the Braun-Blanquet method, which attempts to combine an estimate of plant cover and number of individual plants (Werger 1974), was not used. Instead, a simple percentage cover scale (percentage cover being the proportion of ground covered by the perpendicular projection of all aerial parts of the plant), classifying cover of species in 5 % intervals, was used in order to make the classification less subjective (Werger 1974) and giving equal weighting to all the steps in the cover scale. In this way, percentage cover can be used as a measure of abundance of a particular species (Digby & Kempton 1987).

Habitat characteristics

Apart from the usual identifying relevé information such as locality in GPS coordinates, date of sampling, and size of plots, the following were also noted: altitude, aspect and slope, percentage litter cover, percentage bare soil, and percentage surface rock. A general description of the habitat where the relevé was done, was also given.

Species diversity, evenness of species distribution and species richness

The percentage cover of each species per plot and the total number of species in each plot obtained from the Braun-Blanquet sampling strategy was used to calculate the Shannon-Wiener species diversity index, evenness of species distribution, and species richness, for each sampling plot. These three values were then used as an additional indication of the effects of different soil characteristics and management strategies on the vegetation in the study area.

Soil sampling and analysis

Sampling design

Three randomly-selected soil samples within each of the Braun-Blanquet classification plots were combined to form one composite soil sample for each plot. The top layer of plant debris and stones was removed and the soil sample was taken from the top 20 cm of soil.

Chemical analysis

All the soil samples were air dried and sieved through a 2 mm mesh size, before any analyses were done. The following measurements were taken: pH, conductivity and percentage organic carbon for all soil samples, and available phosphorus, exchangeable cations (sodium, potassium, calcium, magnesium), and total nitrogen for a subset of 15 soil samples (see below for details).

Soil pH was measured in a 1 mol/dm^3 KCl solution using a Corning pH meter 430 (Anonymous 1990). All reported pH values are therefore pH in KCl. Conductivity was measured in a 1:5 soil:water ratio saturation extract (Rhoades 1982) using a Corning conductivity meter 441. All soil samples were tested for the presence of inorganic carbon in the form of $CaCO_3$ (which occurs in parts of the study area), with concentrated hydrochloric

acid according to the method described by Nelson & Sommers (1982). The South African protocol for the Walkley-Black technique (Anonymous 1990) was subsequently used to determine organic carbon content for all the soil samples. This method was decided on because of the calcareous nature of some of the soils, meaning that the presence of inorganic carbon in the form of carbonates can be misinterpreted as organic carbon when other methods such as weight-loss upon ignition, is used (Nelson & Sommers 1982).

Available phosphorus, exchangeable cations and total nitrogen were determined by a professional laboratory, BEMLAB BK, Somerset West, South Africa. The following methods were used: (1) Available phosphorus - Bray II method (Bray & Kurtz 1945); (2) Exchangeable cations (Ca, Mg, K and Na) were measured using a 1 M ammonium acetate extraction with subsequent determination of cation levels using a flame or gas photospectrometer (Doll & Lucas 1973) and; (3) Total nitrogen was determined by digestion in a LECO FP-528 nitrogen analyser.

Structural/physical analysis

All soil samples were structurally analysed using finger texturing methods (Anonymous 1986) and verified with the USDA (United States Department of Agriculture) classification scheme (Gee & Bauder 1986). Percentage rock (particles larger than 2 mm) in each soil sample was determined by sieving (2 mm mesh size) and subsequent weighing of the rock fraction. This fraction will subsequently be referred to as percentage internal rock.

Water-holding capacity of the different soil types was determined through comparisons of the volume of water contained in each soil type at saturation level. A saturation paste was made up (Rhoades 1982) and the percentage water contained by each soil sample at saturation was used as an indication of the potential amount of water that a soil can contain.

Grazing strategies

Grazing strategies on each of the ranches forming part of the study area were determined by personal communication with the various landowners and managers in the area. Grazing strategies were classified as either grazing by cattle or game or as communal grazing.

Statistical analyses

Randomisation tests

The Shapiro-Wilk W test for normality was used to test data for normality of distribution. This test was chosen because of its higher power as compared to other tests (Shapiro et al. 1968). None of the data sets (Braun-Blanquet vegetation data, soil data, and species diversity, evenness of species distribution and species richness data) were normally distributed and the data could not be normalised using transformations. Randomisation (also called permutation) tests (Good 1994) were therefore used in all the statistical analyses, except where canonical correspondence analysis was used (see "Correspondence analysis" below).

Inter-correlations between continuous soil variables were determined by means of the randomisation equivalent of linear regressions, and between continuous and nominal variables by means of the randomisation equivalent of ANOVA with post-hoc tests in which p-values were adjusted with Bonferroni adjustments. Similarly, the relative importance of the continuous soil variables in predicting community composition, were determined with randomisation correlations and that of nominal variables were determined by means of randomisation ANOVA equivalents with post-hoc tests and Bonferroni adjustment. The same analyses were used to determine correlations between percentage organic carbon or management strategy, and percentage cover of plant functional types. Correlations between organic carbon and species diversity, evenness of species distribution and species richness were determined by means of a linear regression (again randomisation equivalent). The effects of soil texture type and management strategy on these variables were determined by means of ANOVA (randomisation equivalents).

Correspondence analysis

Canonical correspondence analysis (CCA), a multivariate, direct gradient analysis technique, was used to directly relate species composition to measured environmental, soil and management variables (Palmer 1993). The technique identifies an environmental basis for community ordination by detecting the patterns of variation in community composition that

can be best explained by the environmental variables (ter Braak 1986). In general, CCA performs much better than other correspondence analysis (CA) techniques i.e. detrended correspondence analysis (DCA). The ability of CCA to perform well with nonorthogonal (when the most important gradients are correlated with each other) and collinear (a large number of included variables are highly intercorrelated) variables, as in the case of this data set, (Palmer 1993) makes it ideally suited for use in this study.

Data were log_{10} transformed before canonical correspondence analysis and the importance of rare species were down-weighted in the analysis. The nominal variables aspect, grazing strategy and soil texture class were dealt with as dummy variables, for example in the case of grazing strategy, two dummy variables 'cattle' and 'game' were identified – the variable 'cattle' takes the value of 1 when a plot has been grazed by cattle, and a value of 0 when otherwise. The variable 'game' is defined analogously. A plot grazed in the communal area thus scores the value 0 on each of the two variables. The canonical coefficient of 'cattle' then measures the difference in expected site scores between grazing by cattle and communal grazing. The same procedure was used for the variables aspect and soil texture type (ter Braak 1986).

CCA results in an ordination diagram (see Figure 3-1) with species and/or site scores as points in the diagram and can be interpreted as follow: Arrows represent continuous environmental, soil and management variables. The length of an arrow indicates the importance of the variable, the direction indicates how well the variables are correlated with the various species composition axes, the angle between arrows indicates correlations between variables, the location of site scores relative to arrows indicates the environmental characteristics of the sites, and the location of species scores relative to the arrows indicates the environmental preferences of each species (ter Braak 1986; Palmer 1993). Nominal variables are plotted as centroids. Distance from centroids indicates environmental characteristics of sites, and location of species scores relative to the centroids indicates the environmental preferences of each species (Kovach 1999).

4. Results

Inter-correlations between soil and management variables

Many of the measured soil and management variables were expected to be correlated and to therefore have joint effects on plant species distribution in the study areas. Such intercorrelations between the continuous variables and between continuous and nominal variables were investigated with randomisation tests with 1 000 iterations. The results of the randomisation regression equivalents are given in Table 3-1 and any trends in the levels and distributions of organic carbon, pH, conductivity, water-holding capacity and rockiness under the three management strategies (cattle, game, communal), in areas where $CaCO_3$ was present or not, and on different soil texture types, are discussed below.

Table 3-1: Correlation coefficients (r) and significance of these correlations (p) between different soil, environmental and management variables. Significant correlations are indicated in bold.

Variables	Organic C (%)	Conductivity (µS/cm)	Water-holding capacity (%)	Internal rock (%)	Surface rock (%)
pH	**r = 0.64** **p < 0.001**	**r = 0.49** **p < 0.001**	**r = 0.62** **p < 0.001**	**r = 0.24** **p < 0.001**	r = 0.11 p = 0.10
Organic carbon (%)		**r = 0.35** **p < 0.001**	**r = 0.78** **p < 0.001**	**r = 0.26** **p = 0.01**	**r = 0.16** **p = 0.04**
Conductivity (µS/cm)			**r = 0.38** **p < 0.001**	**r = 0.25** **p = 0.03**	r = 0.14 p = 0.08
Water-holding capacity (%)				r = 0.11 p = 0.12	r = 0.11 p = 0.12
Internal rock (%)					**r = 0.48** **p < 0.001**

Organic carbon

Percentage organic carbon present in the soil did not differ significantly with management strategy (p = 0.07). Percentage organic carbon was, however, significantly higher in areas where $CaCO_3$ were present (mean percentage organic carbon = 0.86), than in areas where it was not (mean percentage organic carbon = 0.40). There was a general increase in percentage organic carbon as soil texture changed from sand to clay soil. Sands had the lowest levels of organic carbon (mean percentage organic carbon = 0.29) and increased significantly

$(p < 0.001)$ until it reached the highest levels in the clay soil (mean percentage organic carbon $= 0.85$).

pH

Soil pH did not differ significantly in areas under the different management types ($p = 0.483$). As can be expected though, pH was significantly higher in areas where $CaCO_3$ was present (mean pH $= 7.57$) than where it was absent (mean pH $= 5.40$). Clay soils had a significantly higher pH (mean pH $= 7.00$) than any of the other soil texture types ($p < 0.001$). Although the sands had the lowest pH (mean pH $= 5.10$), it did not differ from that found in the other soil texture types except for that found in sandy-clay-loam (mean pH $= 5.91$; $p = 0.001$) and clay soils ($p < 0.001$).

Conductivity

None of the three management strategies influenced conductivity in the soil significantly ($p = 0.553$). Conductivity did, however, differ significantly ($p < 0.001$) depending on whether $CaCO_3$ was present in the soil or not (mean conductivity: $CaCO_3$ present $= 132.01$, $CaCO_3$ absent $= 35.23$). Conductivity was significantly lower in sandy areas than in areas with high clay contents ($p = 0.014$). There was a general increase in conductivity as the clay content of the soil increased, with clay soils exhibiting extremely high levels of conductivity relative to the other soil texture types (mean conductivity: sand $= 26.22$, loamy-sand $= 32.62$, sandy-loam $= 32.65$, sandy-clay-loam $= 44.61$, sandy-clay $= 44.86$, and clay 120.20).

Water-holding capacity

Management strategy did not influence water-holding capacity significantly ($p = 0.544$). Water-holding capacity was, however, significantly higher in areas where $CaCO_3$ was present (mean percentage water-holding capacity $= 20.27$), than where it was absent (mean percentage water-holding capacity $= 15.68$). Sand had the lowest levels of water-holding capacity (mean percentage water-holding capacity $= 15.09$) and clay soils the highest (mean percentage water-holding capacity $= 20.01$).

Percentage Internal-rock

Percentage internal rock did not differ significantly between areas under different management strategies. It seems however that the areas with $CaCO_3$ present had significantly higher levels of internal rock ($p = 0.013$) (mean percentage internal rock $= 7.20$) than those

areas that did not have any $CaCO_3$ (mean percentage internal rock = 3.56). Sandy soils had the lowest levels of internal rock (mean percentage internal rock = 1.23) which differed significantly from soils with a high clay content (p = 0.004), i.e. sandy-clay-loam, sandy-clay and clay (mean percentage internal rock sandy-clay-loam = 6.62, sandy-clay = 6.92 and clay = 5.88).

Percentage surface rock

There were no significant differences in percentage surface rock between areas under different management strategies (p = 0.149), in areas where $CaCO_3$ was present or absent (p = 0.826), or on different soil texture types (p = 0.154).

Further correlations

Further correlations were tested for between pH, organic carbon and conductivity (as measured for all soil samples), and H^+ ion concentration, phosphorus, nitrogen and exchangeable cations (calcium, magnesium, sodium, potassium), as measured for a subset of 15 soil samples. All the variables (phosphorus, nitrogen and exchangeable cations (calcium, magnesium, sodium, potassium)), were correlated with at least one of the variables pH, percentage organic carbon and conductivity (Table 3-2).

Table 3-2: Correlation coefficients (r) and significance of these correlations (p) between different soil variables. Analysis shows levels of N (%), P Bray II (mg/kg) and exchangeable cations (cmol(+)/l) to be correlated with pH, organic carbon (%) and conductivity (μS/cm). Significant p values are indicated in bold.

Variables	P	N	Ca	Mg	Na	K
pH	r = 0.65 p < 0.001	r = 0.69 p < 0.001	r = 0.46 p = 0.040	r = 0.37 p = 0.071	r = 0.28 p = 0.224	*r = 0.43* *p = 0.054*
Organic carbon	r = 0.02 p = 0.412	r = 0.94 p < 0.001	r = 0.73 p = 0.021	r = 0.69 p = 0.010	r = 0.22 p = 0.140	r = 0.77 p = 0.011
Conductivity	r = 0.16 p = 0.231	r = 0.70 p = 0.010	r = 0.22 p = 0.173	r = 0.29 p = 0.141	r = 0.78 p = 0.013	r = 0.26 p = 0.174

Correlations between plant species and soil, environmental and management variables

CCA showed that 49.7 % of the variance in the data was explained by the first two community composition axes. Figure 3-1 shows the main pattern of variation in community composition that can best be explained by the environmental, soil and management variables (for simplicity only species scores are plotted in Figure 3-1). The main species groupings occurred around soil texture, specifically sand or clay soil, with low or high levels respectively of organic carbon, conductivity, pH, and water-holding capacity, as well as phosphorus, nitrogen and the exchangeable cations calcium, magnesium, sodium and potassium, associated with each. The first species grouping occurred on the sandy soils and these habitat types can be described as *Acacia erioloba* E. Mey, parklands. This species grouping was also associated with communal grazing on Figure 3-1. The second species grouping occurred around the clay soils. Figure 3-1 indicates that the clay soils in the study areas are associated with the presence of $CaCO_3$, thereby explaining the high pH levels found in these areas. Soils with high levels of organic carbon, as an indication of organic matter content, would be expected to exhibit high water-holding capacities due to the hydropylic characteristics of organic matter (Barber 1984) and also high levels of conductivity due to the positive effect that organic matter has on the cation exchange capacity of a soil (Tisdale et al. 1990). These habitat types where clay soils with $CaCO_3$ and high levels of pH, conductivity, water-holding capacity, organic carbon and nutrients were found, can be classified as the clay-pan habitats in the study area. There occurred a third species grouping around the second CCA axis that appeared to be associated with the rockiness of the soil rather than with soil texture, levels of organic carbon, conductivity, water-holding capacity and pH. This is confirmed by the fact that these variables were only weakly correlated, if at all (Table 3-1). Most woody species tended to occur in these areas. The fourth species grouping consisted of the remaining species which were clustered around the origin of the CCA diagram and showed no tendency to occur on a specific soil texture type or on very high or low levels of the various continuous soil variables.
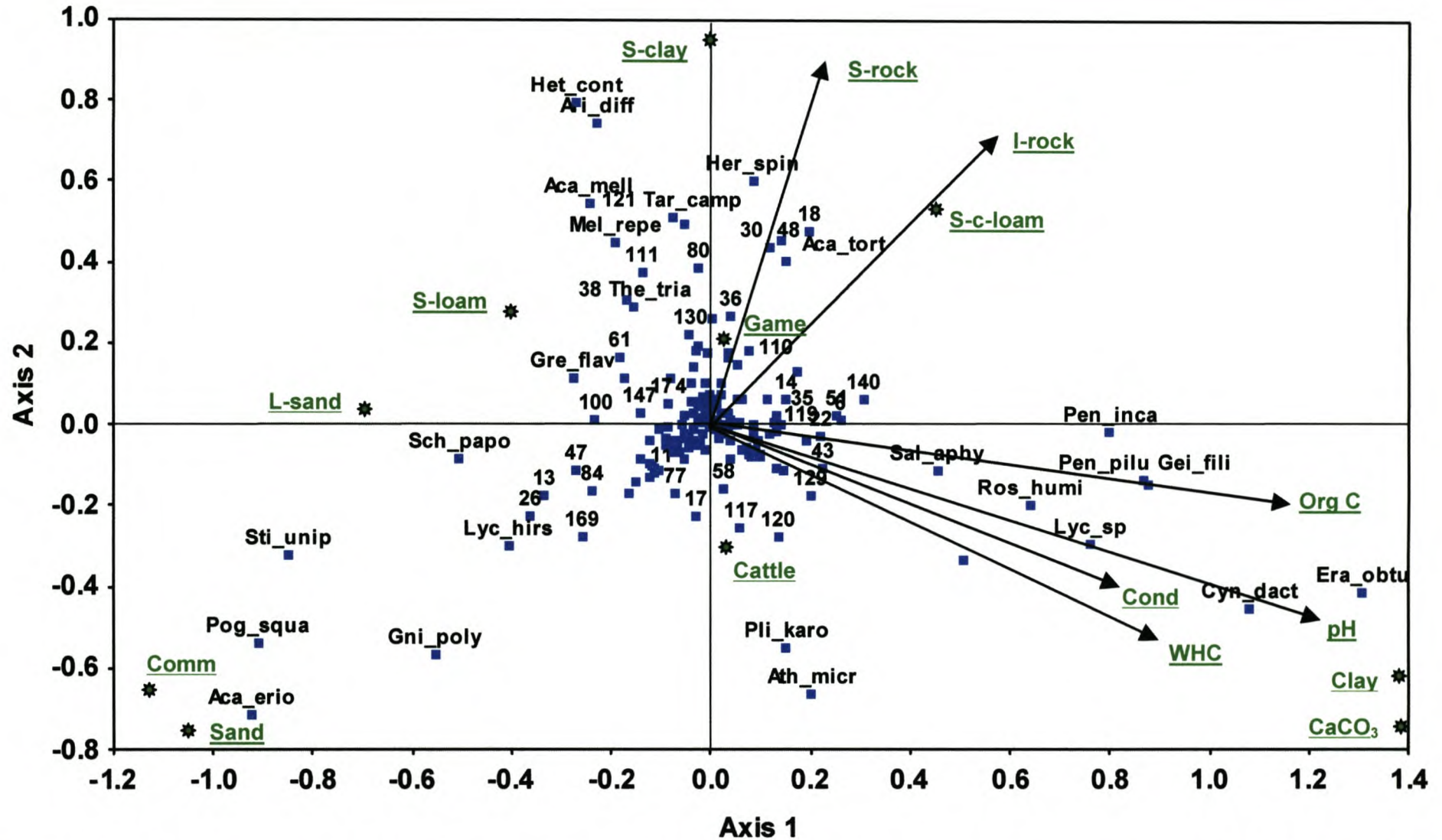
Figure 3-1: CCA diagram showing the correlation between the most important soil and management variables and plant community composition. Continuous variables are plotted as arrows, arrowheads indicating direction of increase. Nominal variables are plotted as centroids ✻ , species are plotted as ■ , with species given code names or numbers as readability allowed. See Appendix 1 for index of code names, numbers and full explanation of variable names. See "Statistical analyses" for details on interpretation.

The relative importance of the continuous environmental and soil variables in predicting community composition, may be inferred by examining the significance, signs and the relative magnitudes of the intraset correlations of the continuous variables, as given in Table 3-3 (intraset correlations being correlations between the environmental and soil variables, and the ordination axes). The intraset correlations were used instead of the canonical coefficients because these will give different results when the environmental variables are correlated with each other, as in the case of this study. Intraset correlations are, however, not influenced by this phenomenon and can therefore still be interpreted accurately (ter Braak 1986). Randomisation equivalents of ANOVA, with post-hoc tests, were used to test the effect of the categorical factors: presence of $CaCO_3$, grazing strategy and soil texture type, on vegetation composition in the study area. These are discussed below.

All the continuous variables were correlated (randomisation tests with 1 000 iterations) with community composition axis one, with the exception of altitude, which was not correlated with CCA axis 1 or 2, and aspect which was only very slightly correlated with CCA axis 2. These two variables will therefore not be discussed further.

Table 3-3: Significance of correlations between CCA community composition axes 1 and 2, and continuous soil variables. Significance indicates the degree to which the specific variable influences plant community composition. Significant correlations are indicated in bold.

Variable	CCA community composition axis 1	CCA community composition axis 2
pH	**r = 0.84** **p < 0.001**	r = - 0.35 p = 1.000
Organic carbon (%)	**r = 0.80** **p < 0.001**	r = - 0.20 p = 0.992
Water-holding capacity (%)	**r = 0.61** **p < 0.001**	r = - 0.35 p = 1.000
Conductivity (µS/cm)	**r = 0.53** **p < 0.001**	r = - 0.29 p = 1.000
Internal rock (%)	**r = 0.38** **p < 0.001**	**r = 0.47** **P < 0.001**
Surface rock (%)	**r = 0.17** **p = 0.022**	**r = 0.60** **P < 0.001**

Of the continuous soil variables, pH and organic carbon were the most important factors influencing community composition and their effects were seen on the first CCA axis only. Thereafter, water-holding capacity and conductivity also had a marked effect on community composition. Rockiness showed the greatest effect on community composition on the second CCA axis, with surface rock having a greater effect than internal rock.

Of the categorical factors (presence of $CaCO_3$, management strategy, and soil texture type), vegetation composition under communal grazing differed significantly from that found in areas under cattle and/or game grazing on the first CCA axis ($p < 0.001$). A post-hoc test showed that vegetation composition did not differ significantly between areas grazed by cattle and those grazed by game (axis 1, $p = 0.846$; axis 2, $p = 0.070$).

Of the soil texture types, sand and clay soils had the most pronounced effects on species composition on the first CCA axis (see also Figure 3-1). Species composition differed significantly between these two soil texture types ($p < 0.001$). Post-hoc tests indicated that species composition also differed significantly between sand and clay soils and all the other soil texture types. It must be noted that although some of the other soil texture types (sandy-clay-loam and loamy-sand) also had slight effects on community composition, the effects of clay and sandy soils were by far the greatest and were noticeably different from each other, probably due to differences in the levels of pH, organic carbon, water-holding capacity and conductivity found on these two soil texture types, and the strong effects these last mentioned variables has on community composition.

$CaCO_3$ also influenced vegetation composition significantly on the first and second CCA axes, and vegetation composition differed significantly depending on whether $CaCO_3$ were present in an area or not (axis 1: $p < 0.001$; axis 2: $p < 0.001$).

Correlations between organic carbon, other soil variables, management strategies, and vegetation

Correlations between organic carbon and pH, water-holding capacity, conductivity, soil texture and CaCO₃

The variables organic carbon, pH, conductivity, water-holding capacity, soil texture and the presence of $CaCO_3$, were all correlated with each other. The effects of the correlations can be seen in Figure 3-1. High levels of the above-mentioned continuous variables occur, together with clay soils and $CaCO_3$, all grouped at the one end of the CCA diagram. Low levels of these variables occur in conjunction with sandy soils at the opposite end of the CCA diagram. Because of the importance of organic carbon in determining community composition in the study area (Table 3-3), the correlations between organic carbon and the above-mentioned soil variables (Tables 3-1 and 3-2), and the fact that organic carbon is a key attribute and good indicator of overall soil quality (high levels indicating good soil quality - Gregorich et al. 1994; Reynolds et al. 2002), percentage organic carbon was used as an indicator of the effects of all the other correlated variables, pH, conductivity, water-holding capacity, exchangeable cations, soil texture (effects of sand and clay soils) and the presence of $CaCO_3$, on community composition.

Relationships between percentage organic carbon, management strategy, and percentage cover of plant functional types

Woody vegetation

Randomisation equivalents of a linear regression indicated that, when all plots were included in the analysis, percentage cover of woody vegetation was negatively correlated with percentage organic carbon ($r^2 = 0.09$, p =0.001). This implies a negative correlation between percentage cover of woody vegetation and the other soil variables too, as explained above. Woody vegetation occurred sparsely in areas with high levels of organic carbon and did not occur on the clay pans in the study area at all. This trend was observed for N_2-fixing species (in this case *Acacia* species) as well as non-N_2-fixing species. When the plots done in the clay-pan habitats were removed from the analysis, woody vegetation was not significantly correlated with percentage organic carbon (p = 0.640). The most dominant woody species (those with the highest percentage cover) in the study area (in order of dominance) were:

Tarconanthus camphoratus L. [*T. minor* Less.], *Acacia mellifera* (Vahl) Benth. subsp. *detinens* (Burch) Brenan, and *Grewia flava* DC., followed by *A. tortilis* (Forsk.) Hayne subsp. *heteracantha* (Burch.) Brenan, and *A. erioloba*. *T. camphoratus* (r^2 = 0.05, p = 0.008), *A. erioloba* (r^2 = 0.08, p < 0.001) and *A. mellifera* (r^2 = 0.03, p = 0.06) were very slightly negatively correlated with organic carbon. *G. flava* (p = 0.23) and *A. tortilis* (p = 0.87) showed no significant correlation with organic carbon.

Randomisation equivalents of ANOVA indicated that percentage cover of woody vegetation was significantly higher under communal grazing than under cattle grazing (p = 0.025; mean percentage cover of woody vegetation: cattle grazing = 19.59, communal grazing = 34.52). Percentage cover of woody vegetation under game grazing was higher than that found under cattle grazing and lower than that found under communal grazing, although it did not differ significantly from either of these values (p = 0.20; mean percentage cover of woody vegetation: game grazing/browsing = 26.74). The dominant woody species responsible for the significantly higher levels of woody vegetation in communal areas are, in order of dominance: *A. erioloba*, *T. camphoratus*, and *G. flava*. *A. mellifera*, an encroaching species in the study area, also occurred in relatively high percentages, but the levels found in communal areas was not significantly different from those found in the cattle and game areas (p = 0.20).

Grassy vegetation

Percentage cover of grassy vegetation showed no correlation with percentage organic carbon (r^2 < 0.001, p = 0.92). The dominant grass species in the study area, in order of dominance, were: *Schmidtia pappophoroides* Steud., *Eragrostis lehmanniana* Nees, *Aristida congesta* Roem & Schult. and *Cynodon dactylon* (L.) Pers. Of these species, *E. lehmanniana* and *A. congesta* showed no specific preference in terms of organic carbon, but percentage cover of *S. pappophoroides* was negatively correlated (r^2 = 0.24, p < 0.001), and that of *C. dactylon* was positively correlated (r^2 = 0.31, p <0.001) with percentage organic carbon. The last mentioned is not surprising seeing that this species is most often found on the clay pans which have high levels of organic carbon and also occurs there more often than any other grass species. It is, however, also found in relatively high percentages on non-clay pan habitats with high levels of organic carbon. Species that never occurred on clay-pans in the study area are: *Stipagrostis uniplumis* (Licht.) De Winter, *Pogonarthria squarrosa* (Roem. & Schult.), *S. pappophoroides*, *Themeda triandra* Forssk., and *Heteropogon contortus* (L.)

Roem & Schult. Other dominant species found in the study area were: palatable species: *Eragrostis obtusa* Munro ex Fical. & Hiern, *Heteropogon contortus, Stipagrostis uniplumis,* and *Themeda triandra,* and less palatable or unpalatable species were *A. diffusa* Trin., *Cymbopogon plurinodis* (Stapf) Stapf ex Burtt Davy, and *Pogonarthria squarrosa.*

Randomisation equivalents of ANOVA indicated that percentage cover of grassy vegetation did not differ significantly under the different grazing strategies (p = 0.865). The only individual grass species that had significantly higher percentage cover values in the communal area than in the other areas is *P.squarrosa* (p < 0.001; mean percentage cover in communal area = 14.15, cattle area = 1.06, game = 1.72). *C. dactylon* occurred in significantly higher levels in the cattle and game areas than in the communal areas (p = 0.02; mean percentage cover in communal area = 0.01, cattle area = 2.14, game = 3.67)

Small shrubs and forbs

There was only a very weak correlation between percentage cover of small shrubs and forbs and percentage organic carbon (r^2 = 0.07, p = 0.001). The small shrubs with highest percentage cover in the study area, *Pentzia incana* (Thunb.) Kuntze, *Felicia fascicularis* DC., did not show any preference for specific levels of organic carbon.

Percentage cover of small shrubs and forbs also did not differ significantly under any of the three grazing strategies (p = 0.101). *G. polycephala,* however, occurred in significantly higher proportions in the communal area than in the cattle or game areas (randomisation equivalent of ANOVA: p = 0.01; mean percentage cover in communal area = 3.91, cattle area = 0.97, game = 0.24).

Correlations between organic carbon, soil texture, management strategy and species diversity, evenness of species distribution, and species richness

There were no significant correlations between species diversity and organic carbon (p = 0.239), but the clay-pans had a significantly lower species diversity than any of the other soil texture types (randomisation equivalent of ANOVA: p = 0.011; mean diversity clay = 0.67, sand = 0.90, loamy-sand = 0.91, sandy-loam = 0.86, sandy-clay-loam = 0.86, sandy-clay = 0.91). Evenness of species distribution was weakly correlated with organic carbon (r = 0.18; p = 0.02) in all areas except in the clay-pans where it was negatively

correlated (r = - 0.21; p = 0.001). Species richness was, however, negatively correlated with organic carbon in all soil texture types, although to a lesser extent in those other than the clay-pans ("other" soil texture types: p = 0.002; r = - 0.24, clay-pans: p < 0.001; r = - 0.41).

Randomisation equivalents of ANOVA indicated that there was no significant difference in species diversity (p = 0.094), evenness of species distribution (p = 0.051), or species richness (p = 0.827) under the three management types. However, when these values were compared for each soil texture type separately, under each grazing strategy, it was found that under game grazing species diversity (p = 0.002), evenness of species distribution (p = 0.041), and species richness (p < 0.001), were significantly lower on the clay soils than on any of the other soil texture types.

5. Discussion

Description of vegetation distribution in the study area

In the study area, *Acacia erioloba*-parkland vegetation is associated with sandy soils, with relatively low pH, organic carbon, water-holding capacity and conductivity, and therefore, relatively low levels of nutrients, as compared to the clay soils in the study area. *A. erioloba* is almost exclusively confined to these sandy areas. In general, woody vegetation with deeper, less efficient root systems, as compared to grasses, can use underground water during the dry season, making them less dependent on available soil moisture in the upper soil layers than grasses (Shelton 1994). Often, sandy soils, with their high permeability, have a water table beyond the reach of all but the longest tap roots, such as those of *A. erioloba* which have been reported to root down to permanent water at great depth (Barnes et al. 1997). In the seedling stages it has been noted that *A. erioloba* exhibits an extremely slow growth rate and this has been attributed to the ability of *A. erioloba* to direct most of its growth into the establishment of an extremely long and strong root system (Shelton 1994). This might explain the dominance of *A. erioloba* in sandy soils, because it may be the only large woody species able to survive the dry season in these habitats. For an explanation on the association of communal grazing strategies with this habitat type, see "Management strategy" below. The grass species occurring in the sandy areas are mostly palatable, perennial, tuft grasses that prefer deep, well drained, sandy soils (*Stipagrostis uniplumis* and *Schmidtia pappophoroides*)

(Bezuidenhout 1994; van Oudtshoorn 1994; Malan et al. 2001). *Pogonarthria squarrosa* (which can be unpalatable), are an indicator of sandy soils with low nutrient content (Bezuidenhout 1994; van Oudtshoorn 1994). Furthermore, *Lycium hirsutum* Dunal, a thorny, woody shrub that is often found under the canopy of *A. erioloba* trees, also appears to be associated with sandy soils (Bezuidenhout 1994). *Gnidia polycephala* C.A. Mey. Gilg, a poisonous plant that often indicates disturbed veld, was also grouped within the sandy habitats. The presence of this species may be a result of communal grazing practised in large sections of this habitat type and under which this species occurred more frequently than on any other management strategy (see "Management strategy" below).

At the other extreme are the calcrete, clay-pan habitats. These clay-pans have a high pH, (due to the presence of $CaCO_3$), as well as high conductivity, water-holding capacity, and organic carbon levels, meaning that they are, by correlation and inference, high in phosphorus, nitrogen and exchangeable cations too. These pans are seasonally inundated, leading to anaerobic conditions during the wet season, and bake hard and crack during the dry season, leading to a harsh soil environment for plant establishment and survival. The texture of these soils also offers high resistance to root penetration. These factors all combine to prevent the establishment of woody species. Indeed, even the grass and small shrub species that occur here are dwarfed in form. This is due to the soil texture, but also to the very heavy levels of grazing by especially plains game, such as Springbok (*Antidorcas marsupialis*), that frequents areas with sparse low vegetation (Novellie 1990). Nutrient enrichment often occurs in these areas due to the dung and urine of the grazers that often collect on these habitats. Apart from the water regime, species that occur here therefore also need to be adapted to heavy grazing as and trampling and need to be able to grow in nutrient-enriched conditions. The effects of nutrient enrichment in an area can be described by the "paradox of enrichment" (Rosenzweig 1971), which states that diversity is reduced in nutrient enriched areas, but that diversity is maximized at intermediate levels of productivity in an area. The effects of the harsh conditions described above are reflected in the negative effects that clay-pan soils have on species diversity, evenness of species distribution, and species richness. The dominant grasses in the clay-pan habitats, *Cynodon dactylon* and *E. obtusa*, are both perennials and indicators of heavy grazing (van Oudtshoorn 1994). *C. dactylon* is often associated with clay-pans (Anderson & Talbot 1965). It is stoloniferous and rhizomatous (Gibbs Russell & Spies 1988; Vignolio et al. 2002), making it particularly well adapted to shallow soils with high salt contents ($CaCO_3$) and low moisture availability

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(Anderson & Talbot 1965). It can often form dense swards in nutrient-enriched areas and its stolons and rhizomes provide a refuge for nutrient and energy storage during periods of heavy grazing (Gibbs Russell & Spies 1988; Walker et al. 1981). Grasses with a creeping growth habit such as *C. dactylon* are often seen to take over from erect, bunch grasses under heavy grazing (Walker et al. 1981). Although *E. obtusa* is a perennial bunch grass, it often occurs in overgrazed or disturbed areas and is often associated with calcareous (van Oudtshoorn 1994) and clay soils (Bezuidenhout 1994; Malan et al. 2001). Apart from these two grass species, *Pentzia incana,* a karooid shrub (meaning it is often often associated with the Karoo region of South Africa) of the Asteraceae family, is the other dominant species found on the clay pans. *P. incana* is often found on well-drained stony soil (Bezuidenhout 1994), making its dominance on the clay-pans surprising, although it might be because of its resistance to grazing. *Geigeria filifolia* Mattf., another species frequently found on the clay-pans, often occurs on flood plains (Shearing 1994), indicating its preference for poorly drained soils, which, together with the fact that it is a poisonous plant and is seldom grazed, would explain its presence on the clay-pans.

Apart from plant species associated with sandy and clay soils, there was also a group of species that was associated with rockiness, including surface rocks and gravelly soils. The rocky areas had sandy-loam, sandy-clay and sandy-clay-loam soils, containing moderately low to moderately high levels of organic carbon, water-holding capacity and nutrients as the clay content of the soil increases. Most of the woody shrubs and trees found in the study area, fell into this group. These include *Acacia mellifera, A. tortilis, Tarconanthus camphoratus,* and *Grewia flava.* In savannas, woody species are often associated with rocky areas (Scholes 1990). Because of their less efficient root systems as compared to grasses, these species are poor competitors with respect to soil moisture in the upper soil layers. In general, rock fragments on the surface protect the soil surface from sealing and crust formation by the impact of raindrops (Agassi & Levy 1991; Cerda 2001) and compaction (Poesen & Lavee 1994), and thus increase the water infiltration and percolation rates into the soil (Tromble 1976; Poesen & Lavee, 1994; Poesen et al. 1994), making more water available for use by trees. Furthermore, rock fragment content decreases the soil bulk density (Stewart et al. 1970; Cerda 2001) which improves the soil structure of fine textured soils such as sandy-loam or sandy-clay soils (Poesen & Lavee 1994). In general, rockiness therefore produces a more favourable environment for plant growth and specifically woody plant growth. In the Sudan it has been found that *A. tortilis* is generally indifferent to soil type

when it receives sufficient soil moisture (Kenneni & van der Maarel 1990), indicating that increased moisture supply is the main advantage of rocky areas to the growth of woody species as compared to non-rocky areas. The association of the abovementioned woody species (*A. mellifera*, *A. tortilis*, *T. camphoratus*, and *G. flava*), with rocky areas has been found by other authors (Bezuidenhout 1994; Malan et al. 2001; Breebaart et al. 2001). Increased soil moisture might also be advantageous to certain grass species. *Heteropogon contortus* depends on seed recruitment for survival (O'Connor 1991) and it has been shown in Australian pastures that increased water availability increases seedling recruitment of this species (Orr & Paton 1997). The distribution of this species has however been noted to be variable (Gibbs Russell & Spies 1988), although other authors have also noted its preference for rocky areas (McNaughton 1983; van Oudtshoorn 1994). *Themeda triandra* is also found in a wide range of habitats over South Africa (van Oudtshoorn 1994), as is *Cymbopogon plurinodis* which is often found in association with *T. triandra* (van Oudtshoorn 1994). *Aristida diffusa* often occurs in rocky areas (van Oudshoorn 1994).

Management strategy

Grazing strategy did not influence the measured soil characteristics significantly and the results from the CCA indicate that, in the study area, the measured soil variables (i.e. factors that affect soil moisture and nutrient content and availability) have a greater effect on vegetation communities than grazing strategy does. The possible effects of grazing strategy on the vegetation in the study area may, however, be masked by the high inherent variability in rainfall and soil nutrients in semi-arid regions (Ward et al. 1999). Many authors have shown that stochastic environmental variation, especially rainfall, may override or mask the impacts of herbivory on vegetation in semi-arid and arid regions (Ellis & Swift 1988; O'Connor 1985; Venter et al. 1989; Westoby et al. 1989; Milchunas et al. 1989; Behnke & Scoones 1993; Parsons et al. 1997). On the other hand, because the year in which fieldwork was conducted was an above average rainfall year, any degradive effects that the different grazing strategies might have had on the environment, should be clear, if present, because the system would have had the opportunity to "recharge" during these favourable conditions (Sullivan 1996).

In the study area, cattle grazing and game grazing/browsing, does not have any noticeably different effects on species composition. Browsing by game species is often thought to control the recruitment of woody species into the adult, fire resistant stage in savanna (Trollope 1980; Scholes & Walker 1993), but here we did not find any difference in the levels of woody species between these areas. This does not mean that browsers do not control woody seedling recruitment though, because grazing levels within the study area might be of such a nature that grasses outcompete woody seedlings, meaning that woody seedling establishment does not occur, thus accounting for the lack of difference in woody cover. The significantly lower species diversity, evenness of species distribution and species richness found on the clay soils under game grazing, is probably due to the fact that the clay soils in the game area are found within the clay-pan habitats. The difference found in the above variables are therefore more likely to be due to a combination of soil texture, water-regime and heavy grazing in these habitats, than on the effect of game grazing alone.

The difference in community composition in areas under communal grazing, as opposed to those under game and cattle grazing/browsing, might be explained as follow: Communal grazing seems to be associated with the *A. erioloba* parkland habitat types. It is, however, likely that this association is merely an artefact of the fact that a large proportion of the communal area consists of this habitat type, whereas in the cattle and game areas, this habitat type is more equally represented, together with other habitat types. The presence of this habitat type with its associated species in the communal area is therefore not a result of communal grazing. There was, however, a higher percentage cover of woody vegetation in the communal areas than in the cattle or game areas. This can largely be explained by the relatively higher proportions of *A. erioloba,* with its large crown cover, found in the communal areas, as opposed to the relative proportions of this species found in the game or cattle areas. Additionally, percentage cover values of *Tarconanthus camphoratus*, and *Grewia flava* are, higher in the communal area than in the rest of the study area. Seeing that these species can be considered potential encroachers (Skarpe 1990; Hoffman & Ashwell 2001), their presence in relatively higher proportions, although not in high levels in absolute terms, might indicate slight levels of vegetation degradation. Although *Pogonarthria squarrosa*, an unpalatable grass species, is the only grass species that is present in significantly higher cover values in the communal area than in the rest of the study area, its presence might confirm the start of degradation in the communal area. The presence of *Cynodon dactylon* in higher proportions in the cattle and game areas than in the communal

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area, is likely to be due to the fact that clay-pan habitats are not present in the communal area, and this species is positively associated with this habitat type. The only other notable difference in species composition between the communal area and the cattle and game areas, is the presence of *Gnidia polycephela* in significantly higher levels than found in the cattle and game areas. This is a poisonous plant and often indicates disturbed vegetation, again confirming the start of vegetation degradation in the communal area.

Soil characteristics

In general, the important soil variables influencing vegetation species composition, or indicating other factors that influences vegetation species composition in the study area, were pH and organic carbon (which has similar effects), and soil texture. Although the pH of a soil can affect nutrient availability (Hatton & Smart 1984), and although plant species have limited pH ranges in which they can survive (Barber 1984), the pH of a soil is mostly an indication of other factors that influence species composition more directly. In this case, soil pH indicated the presence or absence of $CaCO_3$ and high or low levels of organic carbon in the soil. Soil pH in the study area was also strongly positively correlated with phosphorus, nitrogen and exchangeable cation levels in the soil. Organic matter in the soil, of which organic carbon is an indication, is a direct source of nutrients (Whitehead 2000) and it also positively affects the capacity of the soil to hold cations (Hatton & Smart 1984). In the study area, organic carbon was also positively correlated with the exchangeable cations calcium, magnesium, sodium and potassium and, more importantly, with nitrogen. Organic matter further improves the soil's water-holding capacity, both through its hydrophilic characteristics and through an improvement of the soil structure (Knoepp et al. 2000; Reynolds et al. 2002).

The importance of phosphorus lies in the fact that it is potentially the most limiting nutrient, to especially grass growth, within semi-arid savannas (Tolsma et al. 1987), and specifically within the sandy soils of the Northern Cape semi-arid savannas (Donaldson & Kelk 1970). In general, nitrogen is the nutrient element that leads to the greatest response from vegetation in terms of herbaceous composition and productivity (Le Roux & Mentis 1986; Walker & Knoop 1987; Belsky et al. 1993). The levels in which it is present in the soil is also particularly relevant to the dynamics of N_2-fixing trees *vs* non-N_2-fixing grasses within savannas. Which of these two elements is most important in study area will, however, depend on which one is most limiting within a particular area (Liebig's law of the minimum -

Miller & Gardiner 1998). In the study area, areas which are relatively less limited in terms of nitrogen availability, for example, on soils with high clay contents, N_2-fixing tree species will have no competitive advantage in terms of nutrient acquisition as compared to grasses. In these cases the herbaceous layer should be favoured and the negative effects of grasses on the early growth and survival of woody seedlings (Moshe et al. 2000), will be greater than in nitrogen limited areas. In areas other than the clay-pan habitats, organic carbon also had a positive effect on species diversity and evenness of species distribution because fewer species are limited by nutrient shortages. On the other hand, in nutrient-poor, and specifically nitrogen-poor, sandy soils, N_2-fixing trees will have a considerable advantage above non-N_2-fixing grasses, which will experience the effects of nitrogen limitation, making them poor competitors relative to N_2-fixing woody species.

In addition to the effects of nutrients, the effects of soil texture, specifically clay and sandy soils, on species composition are also important. These are probably due to the effects that soil texture has on moisture content and availability, and the physical effects of soil texture on plant growth, i.e. root penetration and growth. Although sands have the advantage of water infiltrating easily, due to large pore sizes, it also has high evaporative rates due to the large air spaces between the soil particles (Barber 1984). Coarse-textured soils also have little power of raising capillary water from the ground water and little power of holding water for extended periods of time. Consequently, they easily become very dry unless constantly supplied with water, and soil moisture in these soils is only available for use by plants for limited lengths of time (Reynolds et al. 2002). On the other hand, although fine-textured soils have lower water infiltration rates, they also have slower evaporation rates, and these soils tend to take longer to desiccate. Contrastingly, very fine-textured soils, i.e. clays, hold water very strongly due to the tension caused by the immense aggregate surface of the great number of microscopic, plate-shaped, soil particles. This means that a clay soil can hold water so strongly that the plant roots cannot absorb it, thereby experiencing the effects of desiccation although there is more than enough water present in the soil (Barber 1984). Soils with more than half of their particles consisting of clay and silt are also liable to become water-logged in wet weather, preventing access of air needed for root respiration (Reynolds et al. 2002), and in droughts they bake hard, shrink and crack, prohibiting root penetration (Barber 1984).

In the study area, the combination of soil water availability (as a function of soil texture) and nutrient availability, as described above, is important in determining the tree:grass ratio.

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Although soil moisture and nutrients, specifically nitrogen, is generally less limiting in clay soils, woody establishment and growth is prohibited and/or impeded in the clay-pan habitats and soils with high clay fractions, due to two factors. The first is the soil texture that negatively affects root growth and penetration, and the second is the fact that without nutrient limitation, grasses are better competitors for soil moisture in these habitats. Although N_2-fixing woody species have the competitive advantage over grasses in the nutrient-poor, sandy habitats, woody establishment and growth is again impeded or prohibited in these habitats, but this time due to soil moisture limitation.

Heavy grazing on the nutrient rich, clay soils, should therefore not lead to bush encroachment, because woody plant establishment and growth is extremely limited due to the reasons discussed above. In the sandy habitats N_2-fixing woody species should be able to increase once grasses have been removed by heavy grazing. However, woody spesies establishment and growth is water limited in these habitats and grass removal due to heavy grazing should thus not lead to bush encroachment. On the soil types with intermediate levels of clay or sand, a gradient of nutrient and moisture availability exists, being high in soils where the relative amounts of clay are high, and decreasing as the relative amounts of sand increases. Woody plant establishment and growth is not limited on these soil types by either soil texture (clay soils) or soil moisture (sand soils). Heavy grazing in these areas, and the subsequent removal of the competitive effect of the grass component, has the potential to lead to increases in woody plant abundance, i.e. bush encroachment. It is suggested that the potential of an area to become encroached increases as the relative amounts of sand within the soil increases, up to the level where soil moisture becomes the limiting factor to woody plant establishment and growth. This is because increases in the sand fraction of a soil also implies decreases in nutrients. Lower levels of nitrogen in the soils will give N_2-fixing woody species the competitive advantage over non-N_2-fixing grasses, and when the grass layer is removed, woody species are able to encroach. With higher clay, and therefore higher nutrient contents, woody species might still increase once the grass layer is removed, but the additional advantage that N_2-fixation affords woody species, is not applicable, making it more difficult for woody species to encroach. Theoretically, these areas will be able to withstand heavier levels of grazing before encroachment occurs than the soils with higher sand contents.

6. Conclusion

In the study area, it appears that the presence and availability of soil moisture and nutrients in the soil, is more important in determining species composition than management strategy (cattle, game, or communal grazing/browsing). Of the three different management strategies, communal grazing has the greatest potential to cause degradation of the natural vegetation. In the communal area, slight increases in woody plant cover, as well as unpalatable and poisonous species were found. Although degradation in these areas, with their high stocking rates, has not progressed very far, the possibility that slow, long-term degradation is occurring, can not be excluded. If this is the case, it might mean that the relationship between stocking rate and impact on soils and vegetation is not linear in nature, but that a threshold effect exists (Ward et al. 2000).

It is therefore suggested that although soil moisture limits woody plant increases in sandy habitats, even under heavy grazing, over-utilisation can still reduce the usefulness of this habitat type when unpalatable and poisonous plants increase. Above a certain threshold of utilisation, extreme degradation in the form of bush encroachment might even occur in these habitats. The same principle applies to the clay-pan and other clay-soil habitats which are also relatively resistant to bush encroachment, as explained under "soil characteristics". The clay-pan provide an important habitat for certain game species (especially plains game like springbok, zebra and wildebeest) and productivity of a ranch can be increased if game, which can utilise these habitats, are included in addition to cattle.

The habitats with intermediate soil textures (loamy-sand, sandy-loam, sandy-clay-loam and sandy-clay), which are less limited by nutrients and soil moisture presence and availability, should be used more conservatively than the abovementioned sand and clay habitats. Rocky areas on these soil types seems to be especially prone to encroachment due to the higher levels of soil moisture found in these areas.

In general, because moisture limitation is such an important variable determining woody plant abundance in the study area, we suggest that heavy grazing in above-average rainfall years should be limited in all habitats. N_2-fixing species which are more limited by soil moisture than nutrients, will have the opportunity to germinate *en masse* in years that moisture is not

limiting, and if grasses are removed by heavy grazing during these times, N_2-fixers would be able to establish and reach a stage at which grasses will not be able to out-compete them and encroachment may occur.

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Chapter 4

Dynamics of woody vegetation in a semi-arid savanna – with special reference to bush encroachment by *Acacia mellifera*

1. Abstract

Increases in the tree:grass ratio, with accompanying changes in herbaceous composition, called bush/shrub encroachment, is a worldwide phenomenon in savanna regions. This process globally reduces savanna profitability and biodiversity. Although heavy-grazing by livestock is often believed to be the cause, it is clear that the factors and processes involved in bush encroachment, are poorly understood. The short- and long-term effects of soil type and grazing by game, cattle, or communal grazing, on the tree:grass ratio, were investigated by means of vegetation classification and the analyses of sequential aerial photographs. Vegetation classification indicated that *Acacia mellifera* never occurs on clay-pans, and in low numbers only in other clay and sand soils. This trend is ascribed to the soil texture, soil water regimes, and/or heavy utilisation in these areas. Soil rockiness was important in determining the long-term presence and abundance of *A. mellifera* due to better soil moisture conditions. It appears that *A. mellifera* naturally occurs at high density in these areas and that this savanna is governed by patch-dynamic processes. Furthermore, long-term increases in *A. mellifera* in non-rocky habitats were found, although the causes of this remain unclear. Grazing strategy did not prove to be important in determining presence or abundance of *A. mellifera* in the short-, or long-term.

Keywords: Aerial photographs; canonical correspondence analysis; game, cattle, communal grazing; soil texture; soil moisture; soil nutrients; rockiness; long-term trends; patch-dynamic.

2. Introduction

Quantitative and historical assessments indicate worldwide increases in woody plant abundance in grassland and savanna regions during the last 50 – 300 years (Archer *et al.* 1988; Johnson *et al.* 1993). These increases have also been noticed in Africa and South Africa (Kelly & Walker 1976; van Vegten 1983; O'Connor 1985;

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O'Connor & Crow, 2000). Such increases in woody plant abundance, with the accompanying changes in the herbaceous cover and composition of the natural vegetation in grassland and savanna regions, is termed bush, or shrub encroachment (Archer *et al*. 1988; Brown & Archer 1999; O'Connor & Crow 2000; Hoffman & Ashwell 2001). The above-mentioned changes in the tree:grass ratio of savannas have been attributed to the replacement of indigenous herbivores by domestic grazing animals and intense utilisation of the natural vegetation by domestic livestock. Heavy grazing results in reduced fuel loads, and consequently, less frequent and intense fires, reducing the effectiveness of fire in the control of woody vegetation. Furthermore, heavy grazing leads to altered competitive interactions between the woody and herbaceous layers due to the removal of the grass layer (Noy-Meir 1982; Skarpe 1990a; Hoffman & Ashwell 2001). Additionally, climate (i.e. rainfall events of optimal intensity and frequency for the germination and survival of woody seedlings) (Noy-Meir 1982; Ward *et al*. 2000) and also long-term climate change (i.e. increased CO_2 levels and UV-B radiation), in conjunction with the above-mentioned factors (Neilson 1986; Gifford & Howden 2001), have been identified as possible causes of bush encroachment. Although all these factors contribute to increases in the woody component in savanna systems, the causes of and processes involved in bush encroachment, are still poorly understood (Ward 2002).

In some instances, the shift from grassland and open savanna to shrub- or woodland apparently resulted from recent and rapid changes in the structure and abundance of woody species within their historic ranges (Johnston 1963; van Vegten 1983). In other cases, gradual range extensions probably occurred over several decades (Norton-Griffiths 1979; Dublin 1995). Wiegand *et al*. (2002) have hypothesised that bush encroachment in many semi-arid and arid environments is a natural phenomenon occurring in ecological systems governed by patch-dynamic processes. If this is correct, bush encroachment can be seen as a natural and integral part of savanna dynamics. At the landscape scale, these savannas can be seen as stable, persistent systems due to the fact that the landscape consists of many patches in different states of transition between grassy and woody dominance. Bush encroachment, however, remains a pertinent issue in South Africa where savannas contribute greatly to the ranching, ecotourism and conservation, and hunting industries (Grossman & Gandar 1989). Many subsistence cultures in South Africa, especially those dependent on livestock ranching, are also dependent on savanna systems. Increases in the tree:grass ratio, with concomitant changes in species composition (diverse systems change to monocultures (Dean *et al*. 1999),

increases in unpalatable species (Rohner & Ward 1997)), and lowered productivity of the natural vegetation, have serious consequences in the form of reduced productivity of the land, for all of the interested parties. A better understanding of the factors influencing and driving this phenomenon is needed in order to manage savanna ecosystems on a sustainable basis.

In this study, the short-term patterns and processes of bush encroachment by *A. mellifera* (Vahl) Benth. subsp. *detinens* (Burch) Brenan (Leguminosae) [syn. *Acacia detinens* (Burch.) Brenan] were investigated by means of vegetation classification techniques. Of the factors determining savanna structure and function (soil moisture, nutrients, fire and herbivory (Noy-Meir 1982; O'Connor 1985; Knoop & Walker 1985; Skarpe 1992; Solbrig *et al.* 1996)), we focused on the effects of several soil factors and different grazing strategies on the presence and abundance of *A. mellifera*. To determine long-term changes in percentage cover of woody vegetation, specifically *A. mellifera,* in the study area, aerial photograph analyses were used. Similar approaches to the long-term investigation of woody plant dynamics in grassland and savanna regions were followed by Norton-Griffiths (1979), Dublin (1995), Echardt & Biggs (1999) and Echardt *et al.* (2000). The study area where the dynamics of this species were investigated is located near Kimberley, within a semi-arid savanna in the Northern Cape, South Africa (see "Study area" below for more details).

The encroaching species – *Acacia mellifera*

Acacia mellifera, also known as Swarthaak or Blackthorn (Carr 1976; Holz & Schreuder 1989), is frequently regarded as the main encroaching species in heavily-grazed savanna areas and other arid and semi-arid regions in north-western South Africa (van Vegten 1983; Tolsma *et al.* 1987). It is also the main encroacher in the semi-arid savanna region close to Kimberley, Northern Cape, where the study was conducted. *A. mellifera* is, however, not the only species that occurs here that might be/become encroaching (see "Other encroaching species").

A. mellifera is a deciduous, often multi-stemmed shrub or tree (up to 7 m tall, but usually between 1 and 2 m tall), with a long tap-root and an extensive, shallow, lateral root system, which can extend up to 15 m from the stem (Adams 1967). It is a nitrogen-fixing species and root nodules are found from the seedling stage (Adams 1967). *A. mellifera* is a rarely browsed species, especially by livestock, due to the profusion of sharp, recurved thorns

(Carr 1976; Skarpe 1990a). It is difficult to determine the age of *A. mellifera* trees by counting annual-rings as this species is believed to exhibit false rings (Adams 1967). Relative ages can however be obtained by a method described by Adams (1967) which combines the height and shape of individual trees to determine age.

A. mellifera is often associated with *Tarconanthus camphoratus* L. [*T. minor* Less.] and *Asparagus* spp. (Malan *et al.* 2001). It is extremely drought resistant (Carr 1976; Smit 1999) and it prefers deep, sandy or gravelly soil, but its shallow and wide-spreading root system allows it to also grow well in shallow soil (Donaldson 1969; Carr 1976; Smit 1999). Indeed, Malan *et al.* (2001) found that in the south-western Free State Province, South Africa, *A. mellifera* most often occurred on areas with shallow soil, on hill slopes and in rocky habitats. Bezuidenhout (1994) found in the Than-Droogeveld section of Vaalbos National Park, which is a part of the study area, that *A. mellifera* was restricted to rocky hills where andesitic lava rocks covered more than 30 % of the soil surface, on shallow (<0.3 m), well-drained, rocky soils, and also on shallow (<0.3 m), well-drained, rocky soils with surface limestone. This indicates *A. mellifera*'s hardiness and tolerance to harsh habitats.

It is often found that it is the shallow-rooted *Acacia* species, such as *A. mellifera*, that become encroaching, rather than the deep-rooted species (Adams 1967; van Vegten 1983; Tolsma *et al.* 1987). In heavily grazed areas, where competition between the grassy and woody components is reduced, shallow-rooted shrubs and trees have a competitive advantage over deep-rooted species with respect to soil moisture from rainfall (Walter 1939, 1954). This leads to a situation of asymmetrical root competition for soil moisture between the different woody species, leading to an increase in the shallow-rooted species that have more direct access to the moisture supply from rainfall (Skarpe 1990a; Skarpe 1990b). This shallow-rootedness may also mean that these species may have better access to nitrogen fixing *Rhizobium* bacteria with which they form a symbiosis on their roots, as well as a greater root biomass for *Rhizobium* infection, than the deep-rooted species (Tolsma *et al.* 1987). Better access to *Rhizobium* will afford these species with a competitive advantage, with regard to nitrogen fixation, over individuals or species which do not have this symbiosis, or have less access to *Rhizobium* (Jenkins *et al.* 1988). Tolsma *et al.* (1987) found higher levels of nitrogen in the leaves of shallow-rooted *Acacia* species than in the leaves of deep-rooted species and a low retranslocation rate of nitrogen from leaves to perennial twigs before leaf abscission in those species. These authors see this as a possible indication that nitrogen is not

a limiting factor in the growth of shallow-rooted *Acacia* species and may give them a competitive advantage, firstly over the herbaceous layer, but also over the deep-rooted *Acacia* species in the colonization of heavily grazed areas. Its shallow-rootedness and hardiness therefore makes *A. mellifera* an ideal encroacher, especially under circumstances where competition from the herbaceous vegetation is reduced, as in cases where the natural vegetation is heavily grazed.

In areas with invasion by *A. mellifera* (and often with other invading species as well), pure, dense stands of small (mostly 2 - 4 m in height), even-sized shrubs are formed (Carr 1976; van Vegten 1983; Skarpe 1990a; Skarpe 1991). Adams (1967) determined the relative ages of trees in such dense stands in Sudan, in order to test the hypothesis that these dense stands consist of even-aged individuals. He concluded that this was not the case and that the age distribution of *A. mellifera* in such thickets is continuous. This fairly low and uniform stature of woody encroachers is often found, even when the same species grows much taller in nearby, less disturbed vegetation (van Vegten 1981; Skarpe 1990b). Van Vegten (1981) also noted this phenomenon and speculated on the possibility of the occurrence of a special genotype of *A. mellifera* with stunted growth and a short life span in encroaching situations. Another explanation for this phenomenon may be competition for water between the crowded shrubs, reducing growth (Smith & Goodman 1986; Skarpe 1990a; Skarpe 1990b). Indeed, Skarpe (1991) found evidence that, in dense, encroached stands of *A. mellifera*, these shrubs seemed to be limited primarily by intraspecific competition for soil moisture. This indicates that there is intraspecific competition in which the limiting resource (soil moisture) is fully utilized, and any increase in the size of the plants will lead to a corresponding decrease in density (Norberg 1988; Lonsdale 1990). A possible reason for and advantage of this aggregated growth form may be protection from fire damage. *A. mellifera* shrubs always have at least part of their canopy in the flame zone of grass fires. Apart from the fact that grass cover is reduced in situations of encroachment (mostly as a result of the initial heavy grazing and concomitant changes in the soil environment and increased competition from the woody vegetation, which reduces the success of re-establishment and survival of the grassy vegetation), thereby reducing the fire risk, aggregation also provides an efficient protection against fire (Adams 1967; Skarpe 1991). The application of this theory is unfortunately limited due to its weak group selectionist characteristics.
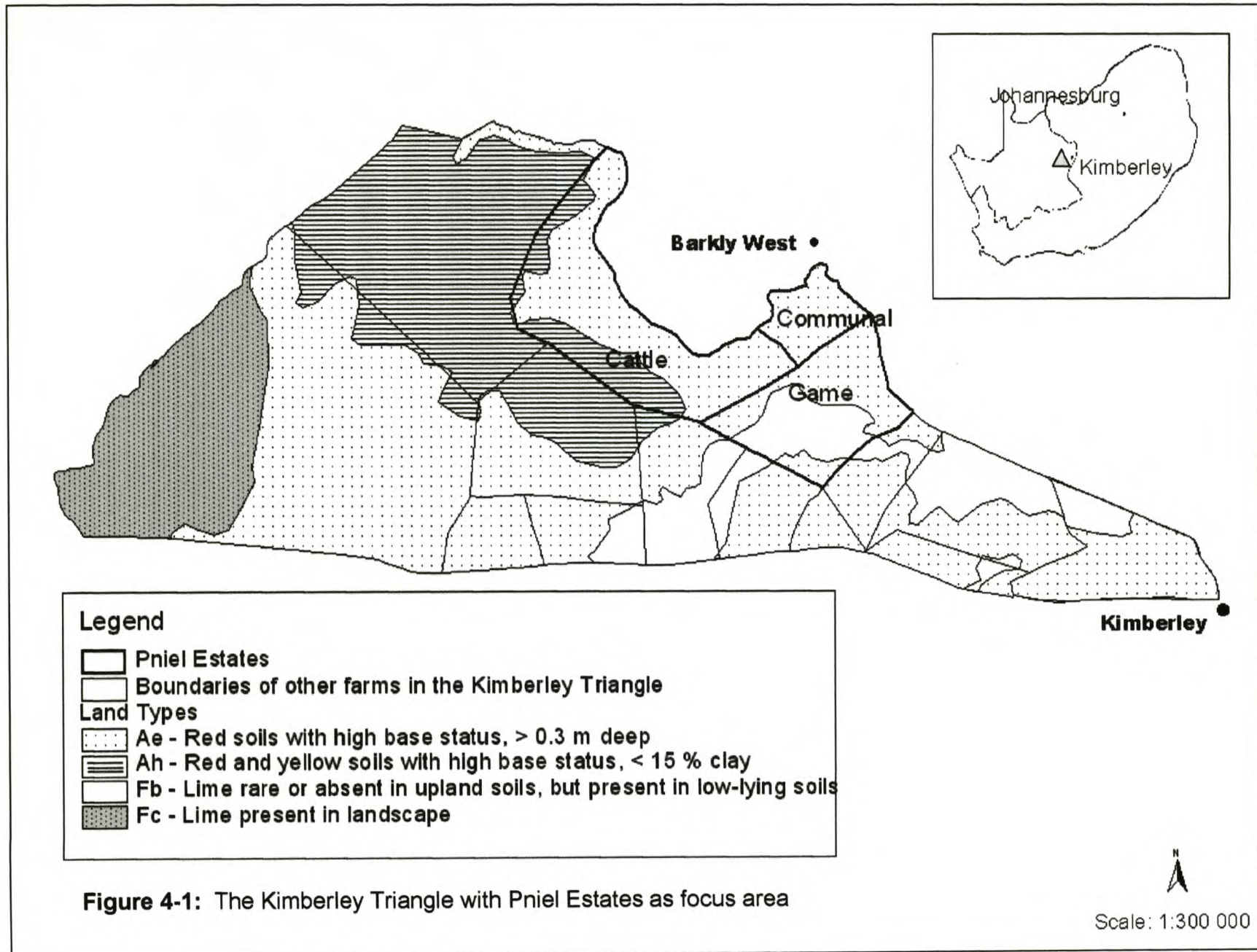
Other encroaching species

Of the woody shrub and tree species that occur in the study area, *A. mellifera* is not the only species that might encroach, although in general only certain species become encroachers while others are unaffected (van Vegten 1983; Tolsma *et al.* 1987; Skarpe 1990b). Species that have been found to encroach in other areas and which also occur in the study area are *A. tortilis* (Scott 1967; Tolsma *et al.* 1987), *Grewia flava* (Skarpe 1990a) and *Tarconanthus camphoratus* (Hoffman & Ashwell 2001). *A. tortilis* and *G. flava* are both shallow-rooted species (van Vegten 1983; Tolsma *et al.* 1987; Skarpe 1990a) as is the case with *A. mellifera*. These species are however not the focus of this project and are only mentioned for the sake of completeness.

3. Materials and methods

Study area

Location

Vegetation classification was carried out in an area of 100 000 ha called the Kimberley Triangle, north-north west of Kimberley in the Northern Cape, South Africa. This is bounded by: 28° 27' 04'' S, 24° 42' 03'' E and 28° 44' 05'' S, 24° 41' 00'' E (see Figure 4-1). The main focus of this study, however, falls on the Pniel Estates, which together with other pieces of land (including the Vaalbos National Park mentioned earlier), owned by private owners, private organizations and the state, forms part of the Kimberley Triangle. Pniel Estates is a 25 000 ha commercial cattle and game farm, owned by the Evangelical Lutheran Church of South Africa. Parts of the farm were leased and heavily grazed prior to 1960, whereafter a multi-paddock system was put into place in the cattle area and since then almost exclusively grazed by cattle (14 000 ha) on a rotational basis at 8 ha per large stock unit. About 15 years ago various species of game were introduced to an adjacent 8 000 ha, and has since been managed for this purpose alone. There is also a 3 000 ha piece of land on Pniel Estates where the Pniel community (150 families) live. This area is a communal grazing area where cattle, goats and donkeys graze (Kraaij 2002).

Figure 4-1: The Kimberley Triangle with Pniel Estates as focus area

Legend

Pniel Estates
Boundaries of other farms in the Kimberley Triangle
Land Types
Ae - Red soils with high base status, > 0.3 m deep
Ah - Red and yellow soils with high base status, < 15 % clay
Fb - Lime rare or absent in upland soils, but present in low-lying soils
Fc - Lime present in landscape

Scale: 1:300 000

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Physiography, geology, soils, and land types

The landscape of the Kimberley Triangle, including Pniel Estates, varies from flat to gently undulating plains and small, andesitic hills. Altitude varies from 1 000 m to 1 250 m above sea level (Bezuidenhout 1994, 1995).

The largest proportion of the Kimberley Triangle and also of Pniel Estates is comprised of red and grey aeolian dune sand, with andesite of the Ventersdorp supergroup often occurring next to the Vaal River but also in extensive patches near the southern border of the study area (Geological Survey 1993). Calcrete and surface limestone occurs in patches in the south-eastern (Pniel Game Ranch) and -western corners of the Kimberley Triangle with an isolated patch in the northern corner. Patches of alluvial, diamondiferous gravel (small patches occurring in the Pniel cattle camp) and small areas of siltstone, shale, quartzite, and gritstone of the Griqualand West sequence occur in the aeolian sand-formations in the northern, and north-western corners of the study area. In addition, in the south-western corner of the study area, an isolated patch of a tillite, sandstone, and mudstone and shale mix, of the Prince Albert formation, Karoo sequence, occurs. In the easternmost corner of Pniel Estates, patches of shale, also of the Prince Albert formation, Karoo sequence, as well as some dolerite intrusions, occur (Geological Survey 1993).

Four land types occur in the Kimberley Triangle (Anonymous 1987; Bezuidenhout 1994, 1995).

    1. The Ae land type: the A unit refers to red-yellow, apedal, freely drained soils, without water tables. The Ae land type refers to red soils with a high base status with a depth of 0.1 to more than 0.3 m.

    2. The Ah land type varies from the Ae land type in that it also includes yellow soil and is consistently deeper than 0.3 m and usually contains less than 15 % clay.

    3. The Fc land type: the F unit refers to land types that usually contains soils from the Glenrosa and, or Mispah forms, although other soils may occur. It further indicates land where the dominant soil-forming processes have been rock weathering, typically giving rise to lithocutanic horizons. The Fc land type occurs in the south western corner of the Kimberley Triangle and refers to areas where lime is usually present in the landscape.

    4. The Fb land type occurs in the eastern parts of the Triangle, and here lime is rare or absent in the upland soils but generally present in low-lying soils (Anonymous 1987; Bezuidenhout 1994, 1995).

Three of the four land types (Ae, Ah and Fb) also occur on Pniel Estates, Ae and Ah in more or less equal proportions, and Fb only occurs in a small isolated area in the eastern corner of Pniel Estates (Anonymous 1987).

Vegetation

The vegetation in the Kimberley Triangle is classified as Kimberley Thorn Bushveld and falls within the savanna biome (Van Rooyen & Bredenkamp 1996). Acocks (1975) classified the vegetation in the study area as Kalahari Thornveld invaded by Karoo (veld type 17), while a small section along the banks of the Vaal River, bordering the study area, consists of False Orange River Broken Veld (veld type 40) (Acocks 1975).

Climate

The study area is part of the summer rainfall region of South Africa. The climate can be described as semi-arid with the long-term (100 years) mean annual rainfall of Barkly West (the closest town to Pniel Estates), being 388 mm. As is often the case in the semi-arid and arid areas, rainfall is extremely variable (C.V. = 39 %), with the 110 year (1892-2002) range: 120 - 980 mm. Precipitation occurs mostly in the form of thunderstorms in the months of January, February and March, with little rain falling from May to October. The total rainfall for the year in which fieldwork was conducted was: January 2001 to January 2002 = 600 mm and for the years for which aerial photographs were obtained: January 1956 to January 1957 = 400 mm, January 1966 to January 1967 = 230 mm and January 1992 to January 1993 = 140 mm. The months of November to February experience daily maximum temperatures exceeding 30°C and can be as high as 44°C. For the remainder of the year the days are warm and in winter the nights are cold (coldest months June-July) and frost occurs (Bezuidenhout 1994; Kraaij 2002).

Data collection and analysis

Data collection: Vegetation, soil and management strategies

Vegetation sampling

To determine the effects of soil and management factors (grazing by cattle, game or communal grazing) on the presence and distribution of *A. mellifera* in the Kimberley Triangle,

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the Braun-Blanquet floristic association method for vegetation classification (Mueller-Dombois & Ellenberg 1974) was used to classify the vegetation communities. Sampling was done on a stratified random basis (Mueller-Dombois & Ellenberg 1974). Sampling was stratified according to ranch, with ranches being representative of grazing strategy on specific soil types. Positioning of sampling plots was done in a way that would make them most representative of the plant community being sampled (see e.g. Ward 2002). Sampling was done from June 2001 to January 2002. Throughout, species nomenclature as by Arnold & De Wet (1993), are used.

Soil sampling

Three randomly-selected soil samples from the top 20 cm of soil within each of the Braun-Blanquet classification plots were combined to form one composite soil sample for each plot. Soil samples were air dried and sieved through a 2 mm mesh size before analyses. The following measurements were taken: $pH_{(KCl)}$ (in a 1 mol/dm^3 KCl solution using a Corning pH meter 430 (Anonymous 1990)); conductivity (in a 1:5 soil:water ratio saturation extract (Rhoades 1982) using a Corning conductivity meter 441), and; organic carbon (%) (Walkley-Black technique (Anonymous 1990)). Furthermore, all soil samples were structurally analysed using finger texturing methods (Anonymous 1986) and results were verified with the USDA (United States Department of Agriculture) classification scheme (Gee & Bauder 1986). Percentage rock (particles larger than 2 mm) in each soil sample was determined by sieving (2 mm mesh size) and subsequent weighing of the rock fraction. This rock fraction will consequently be referred to as "internal rock (%)". Water-holding capacity of the different soil types was determined through comparisons of the volume of water contained in each soil type at saturation level. A saturation paste was prepared (Rhoades 1982) and the volume of water (%) contained by each soil sample at saturation was used as an indication of the potential amount of water that a soil can contain.

Grazing strategies

Grazing strategies on the different parts of the study area were determined by personal communication with the various landowners and managers in the area. Grazing strategies were classified as cattle, game, or communal grazing/browsing.

Data analysis

Effects of soil and management strategy on vegetation

Canonical correspondence analysis (CCA), a multivariate, direct gradient analysis technique, was used to directly relate species composition to measured soil and management variables in the study area (Palmer 1993). The technique identifies an environmental basis for community ordination by detecting the patterns of variation in community composition that can be best explained by the environmental variables (ter Braak 1986). Species (including *A. mellifera*) were plotted together with the measured soil and management variables to show how individual species were distributed relative to these factors (see Figure 4-1) with species and/or site scores as points in the diagram. Arrows represent continuous soil and management variables. The length of an arrow indicates the importance of the variable, the direction indicates how well the variables are correlated with the various species composition axes, the angle between arrows indicates correlations between variables, and the location of species scores relative to the arrows indicates the environmental preferences of each species (ter Braak 1986; Palmer 1993). Nominal variables (i.e. grazing strategy, soil texture type and presence of $CaCO_3$) are plotted as centroids. Location of species scores relative to the centroids indicates the environmental preferences of each species (Kovach 1999).

Because the data used in analyses were not randomly distributed and could not be normalised with transformation techniques, randomisation tests were used in all additional analyses. Randomisation equivalents for linear regressions and ANOVA, with 1 000 iterations, were used to determine trends in percentage cover of the different woody species in different habitat types and under different management strategies, over the time period cover by the aerial photographs (1957 – 1993). Differences in percentage cover values of woody species between the more recent and previous years were determined, bootstrapped (Blank *et al*. 2001), and used as an indication of increasing or decreasing trends. The conventional significance level of $p = 0.05$ was used and accuracy was adjusted with Bonferroni adjustment of p where necessary.

Aerial photograph analyses

Black and white aerial photographs, covering a time span of almost 40 years, taken in 1957 (1:30 000 scale), 1967 (1:60 000 scale) and 1993 (1:50 000 scale), were obtained for Pniel

Estates. The aerial photographs were scanned as grayscale images, all at the same ground-resolution of 45 cm. These images were edited with respect to contrast, shadows and colour in order to make the photographs from different years, taken under different conditions, comparable and to make woody vegetation stand out clearly (Echardt & Biggs 1999; Echardt *et al*. 2000). No georeferencing of aerial photographs was performed because emphasis was on percentage cover of the woody vegetation and not on absolute values (Echardt & Biggs 1999).

Sampling plots were randomly selected within habitat type (rocky: > 15 % surface rock, or non-rocky: 0 % surface rock) for each of the three different management strategies (grazing by cattle, game or communal grazing) for each year. The number of plots per grazing strategy within each of these habitats was unfortunately limited due the availability of aerial photographs for Pniel Estates as well as the number of Braun-Blanquet plots that could be used for ground-truthing. Overall, 15 plots were situated within the game area, nine in the cattle area, but only three could be found in the communal area. This is because the communal area is relatively small, allowing only three plots in rocky areas. In addition, non-rocky habitats in the communal area consisted of *A. erioloba* E. Mey, parklands with deep, red sands, and in the whole of the Kimberley Triangle, *A. mellifera* never occurred in this habitat type. In order to increase statistical power for analysis, the plots in cattle and communal areas were grouped (both areas being used for domestic livestock). Because the aerial photographs were not georeferenced, fixed points that are easily recognisable on the photographs of all three years (e.g. road intersections, prominent trees, rocky outcrops etc.) were identified and used to locate boundaries for the sampling plots. This ensured that the plots covered exactly the same area on the photographs of all three years. Because of the necessity to use recognisable objects to idenitify borders of sampling plots, different plots within each year did not, however, cover the same areas, so that absolute values in woody vegetation cover could not be compared, again placing the emphasis on percentage cover and not on absolute values of woody vegetation. Two important assumptions were made in the selection of aerial photo plots, namely that the vegetation is homogenous enough that vegetation would be the same in the aerial photograph plots as in the Braun-Blanquet plots, and that the soil variables in the Braun-Blanquet sampling plots would be similar to that in the surrounding areas, giving a reliable estimate of the values in the aerial photo sampling plots.

Percentage cover of *A. mellifera* was determined for each plot by means of an unsupervised classification using ERDAS Imagine software (ERDAS Imagine 8.5, ERDAS, Inc.). This software package uses the ISODATA algorithm to recluster data and assign pixels to individual classes. The convergence threshold (the maximum percentage of pixels whose cluster assignments can go unchanged between iterations) was set to 0.95 (Anonymous 1991-2000).

It was found that classifications performed on the grayscale images were limited in ability to differentiate between different species of woody vegetation. *A. erioloba* was the only woody species that could be accurately identified. This was due to its size as compared to other woody species found in the study area. *Acacia mellifera* (the study species), however, occur in the study area in stands mixed with *A. erioloba* and *Grewia flava* DC., among other species. Therefore, plots known to consist of only *A. erioloba* or *G. flava* as the woody component, were identified and tested to determine whether these species showed any significant increase in percentage cover over the years 1957-1993. On the basis of these results (discussed later), a third assumption was made. This is that in sampling areas where *A. mellifera* occurred together with one or both of these species, if an increase in percentage woody cover was noted, it was due to increases in *A. mellifera* only and not due to increases in any of the other species.

4. Results

Factors influencing the presence and levels of *Acacia mellifera* in the Kimberley Triangle

CCA showed that 49.71 % of the variance in the data obtained from the Braun-Blanquet vegetation sampling was explained by the first two community composition axes (Figure 4-2). In the study area, *A. mellifera* occurs on areas of intermediate levels of pH, organic carbon, conductivity and water-holding capacity, and is more often associated with sandy-loam or sandy-clay soil than with any of the other soil texture types. The data obtained from the Braun-Blanquet sampling also showed *A. mellifera* to never occur in the clay-pan or sandy habitats. Furthermore, *A. mellifera* is shown to be associated with areas with high levels (15 – 35 %) of internal rock and intermediate (6 – 15 %) and high (16 – 45 %) levels of surface rock. As can be seen in Figure 4-2, *A. mellifera* does not appear to be associated strongly

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with any of the three grazing strategies in the study area. Indeed, it was determined with the randomisation equivalent of a multiple linear regression, that percentage surface rock is the only measured variable, together with the presence of $CaCO_3$, influencing the percentage cover of *A. mellifera* in the Kimberley Triangle ($r^2 = 0.28$; $p < 0.001$; percentage surface rock β-coefficient = 0.447; $CaCO_3$ β-coefficient = 0.19). Bezuidenhout (1994) also found that *A. mellifera* was often associated with areas with surface limestone. In the data we obtained for the study area (the Kimberley Triangle), however, there were very few sites where *A. mellifera* occurred in association with $CaCO_3$, and these are all grazed by game. Where this did occur, the presence of *A. mellifera* invariably took on encroaching proportions (mean percentage cover of *A. mellifera* for three plots where *A. mellifera* occurred in association with $CaCO_3$ = 45 %).

Furthermore, Figure 4-2 shows that *A. mellifera* is often associated with the woody species *Tarconanthus camphoratus* L. [*T. minor* Less.], and *G. flava*. Malan *et al.* (2001) made the same observation in the south-western Free State Province, South Africa. Figure 4-2 also shows the grass species *Aristida diffusa* Trin., *Heteropogon contortus* (L.) Roem & Schult., *Melinis repens* (Willd.) Zizka, *Themeda triandra* Forssk., and *Eneapogon scoparius* Stapf to be associated with *A. mellifera*. [Note: Figure 4-2 is a duplicate of Figure 3-2 but was re-added in this chapter for clarity purposes].

Trends in percentage cover of *A. erioloba* and *G. flava* on Pniel Estates during the time period 1957 to 1993

Aerial photograph analysis of a stand where *A. erioloba* was the only large woody species, did not show a significant increase in percentage cover between 1957 and 1967 ($p = 0.286$), but did show a significant increase from the 1957-1967 time period to 1993 ($p = 0.012$) (Figure 4-3). Percentage cover levels of *A. erioloba* in 1993 were still low/non-encroaching (mean percentage cover: 7.25 %). The significant increase in percentage cover can be explained by an increase in the canopy size of individual trees and not by an increase in the actual numbers of individual trees (Figure 4-4). *G. flava*, on the other hand, exhibited percentage cover values that might be considered encroaching (mean percentage cover in 1993: 27.18 %). This species did not, however, show any significant increase in mean percentage cover during the period 1957 – 1993 ($p = 0.251$) (Figure 4-3).
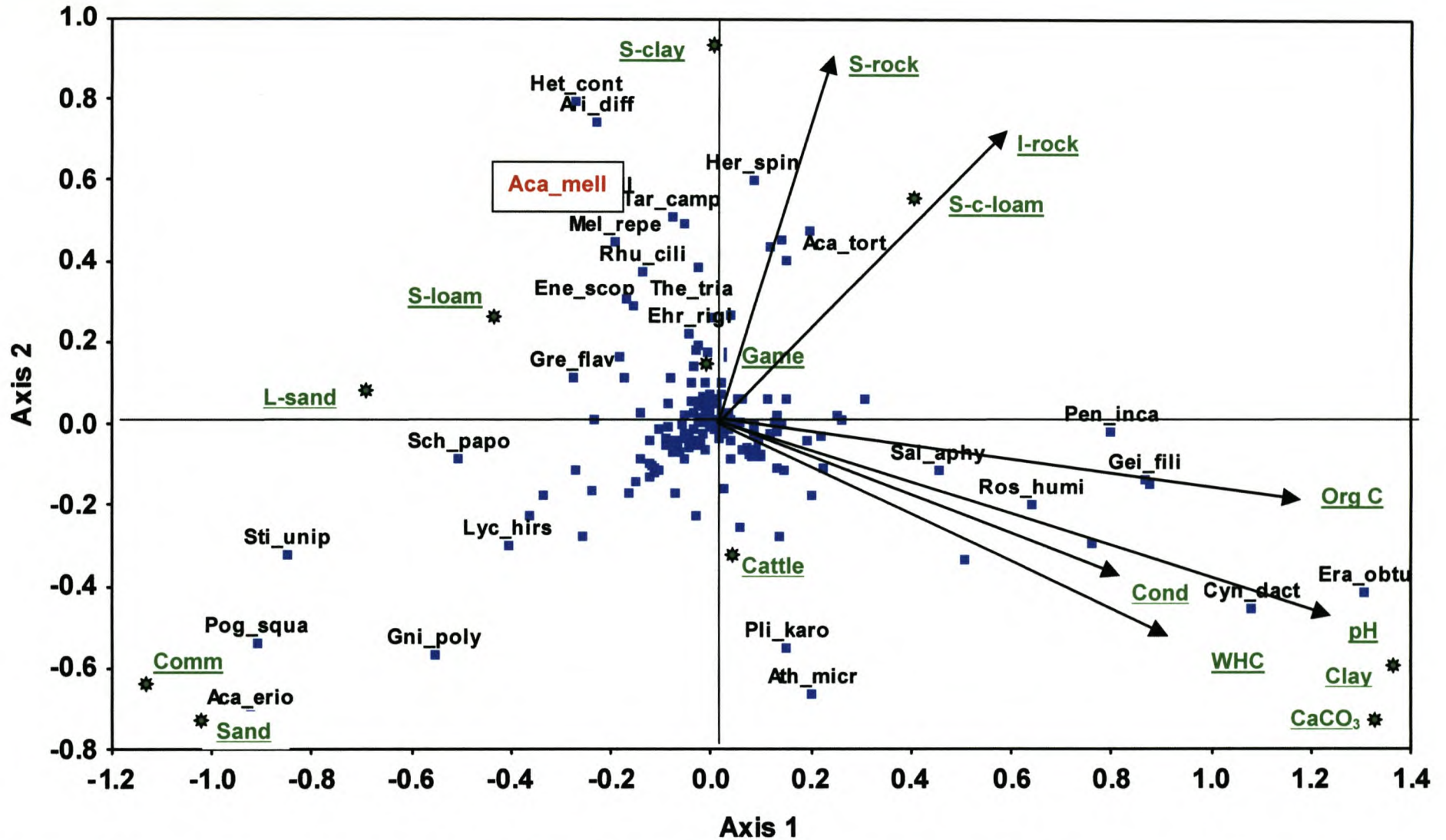
Figure 4-2: CCA diagram showing the association between the most important soil and management variables and the dominant species (including *A. mellifera*). Continuous variables are plotted as arrows, arrowheads indicating direction of increase and length of arrows relative importance in determination of species distribution. Nominal variables are plotted as centroids ✳, species are plotted as ■. See section 2.2.2. "Data analyses", for details. See Appendix 1 for index of code names for species and full explanation of variable names.

In mixed *A. mellifera – G. flava* stands, it can thus be assumed that any increases observed in the percentage cover of woody vegetation are due to increases in the cover of *A. mellifera*, and not due to changes in the other woody species, *G. flava*. In mixed *A. mellifera – A. erioloba* stands, this assumption does not hold true, due to increases in percentage cover of *A. erioloba* during the last 26 years of the time period covered by the aerial photographs. *A. erioloba* can, however, be easily distinguished from other types of woody vegetation in the aerial photograph images, due to its size as compared to the other woody species. By separating pixel classes into those representing *A. erioloba* and those representing other types of woody vegetation, reliable estimates of percentage cover of *A. mellifera* could still be obtained.

Figure 4-3: Mean percentage cover of *Acacia erioloba* and *Grewia flava* on Pniel Estates, as determined from aerial photographs spanning 36 years (1957-1993). *A. erioloba* showed an increase in percentage cover due to an increase in canopy cover of individual trees, as indicated by differences in superscripts. *G. flava* did not show a significant increase in percentage cover during the time period covered by the aerial photographs.
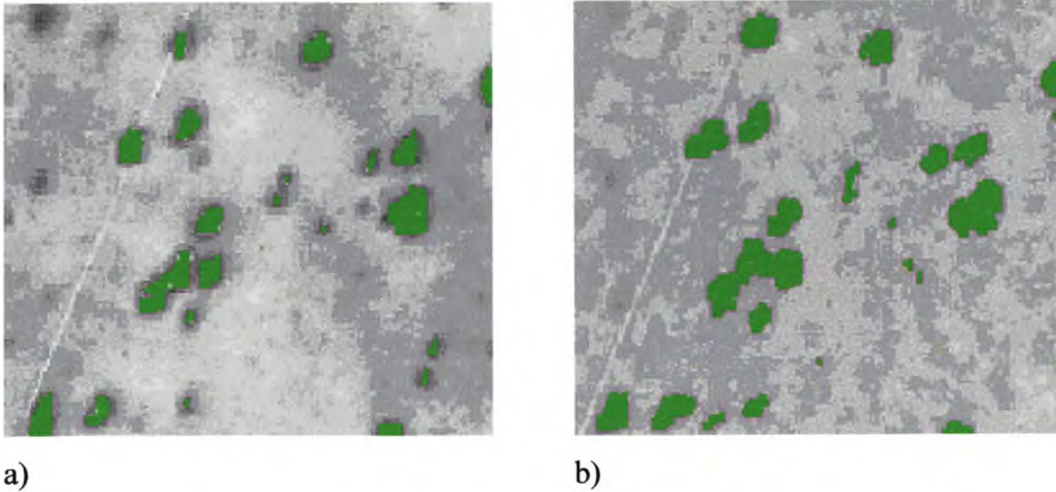
a)   b)

Figure 4-4: Section of a classified aerial photograph showing an increase in percentage cover of *A. erioloba* (green colour) from 1967 (a) to 1993 (b) due to increases in the canopy cover of individual trees rather than due to an increase in the number of trees in the area.

Trends in percentage cover of *A. mellifera* on Pniel Estates, in different habitat types and under different grazing strategies, during the time period 1957 to 1993

Overall, the rate of increase in percentage cover of *A. mellifera* on Pniel Estates was significant from 1957 (p = 0.022; mean percentage cover = 31.12) to 1993 (mean percentage cover = 40.0). The rate of increase of *A. mellifera* was not, however, significant from 1957-1967 (p = 0.208), or from 1967-1993 (p = 0.115), suggesting a gradual, long-term increase. Because rockiness had such a strong effect on the presence and levels of *A. mellifera* in the study area, we tested whether this overall increase was due to an increase in *A. mellifera* in the rocky or in the non-rocky habitats. The aerial photograph analysis showed that in 1957 there was a significant difference in percentage cover of *A. mellifera* between the rocky (p = 0.009; mean percentage cover = 36.50) and non-rocky habitats (mean percentage cover = 22.21). Management strategy within each of these habitats could not be taken into account due to reasons discussed earlier. In 1993, however, this difference between the rocky and non-rocky habitats was not significant (p = 0.288; mean percentage cover in rocky areas = 41.17; mean percentage cover in non-rocky areas = 37.50) (Figure 4-5). The overall increase in percentage cover of *A. mellifera* from 1957 – 1993 is therefore due more to an increase in percentage cover in the non-rocky areas than in the rocky areas. This is confirmed by the fact that

A. mellifera did not increase significantly in the rocky areas during 1957-1993 (p = 0.166; mean percentage cover in 1957 = 36.50 and in 1993 = 41.17), although it did increase significantly in the non-rocky areas from 1967-1993 (p = 0.025; mean percentage cover in 1967 = 25.30 and in 1993 = 37.50) (Figure 4-6).
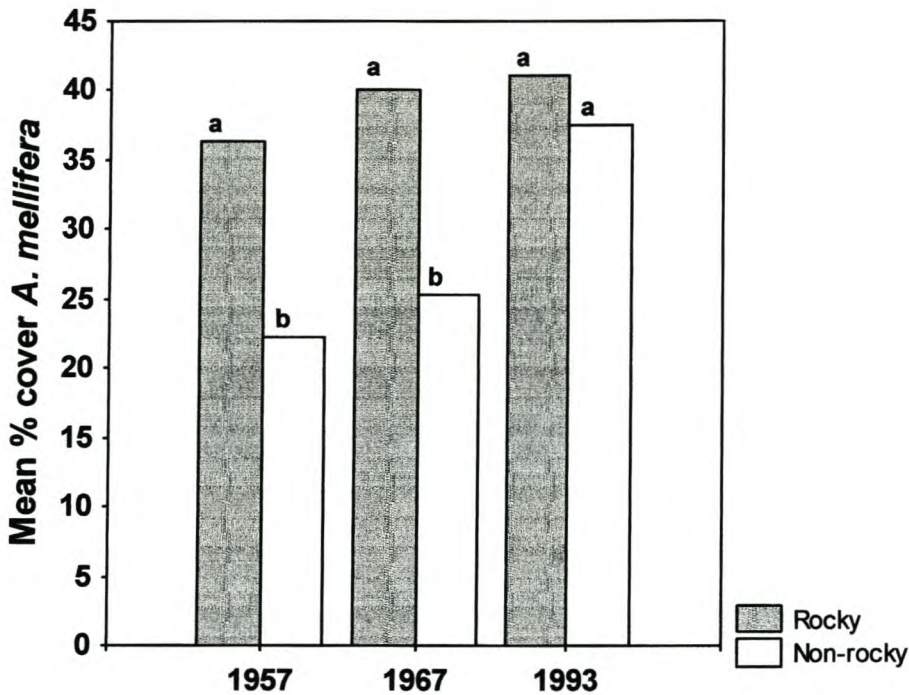

Figure 4-5: Mean percentage cover of *A. mellifera* on Pniel Estates, as determined from aerial photographs spanning 36 years (1957-1993) in rocky and non-rocky habitats. Although in 1957 *A. mellifera* had a significantly higher percentage cover in the rocky than in the non-rocky habitats, this difference disappeared by 1993. Between 1957 and 1993 *A. mellifera* increased more in the non-rocky habitats than in the rocky habitats on Pniel Estates.

a)   b)

Figure 4-6:   Section of a classified aerial photograph showing a significant increase in percentage cover of *A. mellifera* (orange colour) in the non-rocky areas from 1967 (a) to 1993 (b).

When the effects of grazing strategy on the presence and levels of *A. mellifera* are investigated without taking rockiness into account, it is seen that in 1993 there were significantly lower levels of *A. mellifera* in the areas grazed by game than in those with cattle/communal grazing (p = 0.018; mean percentage cover in game area = 33.50; mean percentage cover in cattle/communal area = 46.10). When comparing the percentage cover of *A. mellifera* in 1957 between the areas now classified as being grazed by game or by cattle/communal, but which were then both heavily grazed by cattle, it is seen that even in 1957 (when both areas were grazed by cattle), there were significantly lower levels of *A. mellifera* in the area now grazed by game (p = 0.031; mean percentage cover = 26.3) than in the areas which are now cattle/communally grazed (mean percentage cover = 36.10). Furthermore, there was no significant increase (p = 0.096) in percentage cover of *A. mellifera* between 1957 and 1993 (mean percentage cover changed from 26.3 % in 1957 to 33.5 % in 1993) in areas now grazed by game. On the other hand, the increase from 36.10 % in 1957 to 46.10 % in 1993 found in areas with cattle/communal grazing, was marginally significant (p = 0.051) (Figure 4-7). This increase occurred mainly in the time between 1967 and 1993 (p = 0.061; mean percentage cover 1967 = 36.60 and 1993 = 46.10).
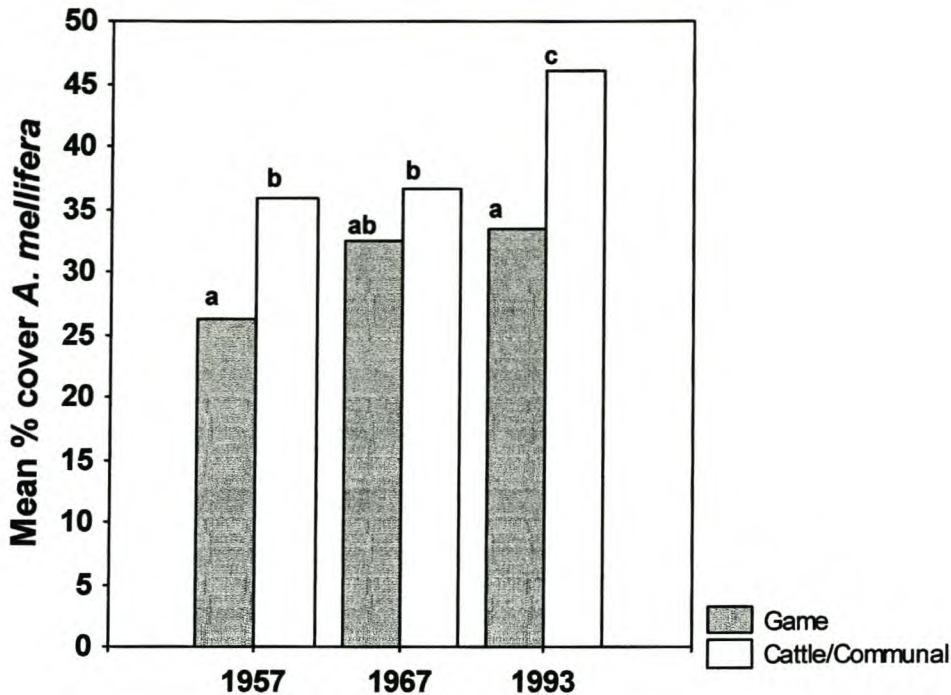
Figure 4-7: The percentage cover of *A. mellifera* was significantly lower in areas now grazed by game than by those areas grazed by cattle from 1957-1993, and only the cattle areas showed any significant increase in percentage cover of *A. mellifera* during this time.

5. Discussion

The absence of *A. mellifera* in areas with high levels of organic carbon, pH, water-holding capacity and conductivity, as well as on clay soils, can be explained by the fact that these conditions are associated with clay-pan habitats found in the study area. This is a harsh habitat for plants to grow in, and not conducive to woody plant growth (Cole 1982). In the study area, the pans are seasonally inundated, leading to excessive moisture levels and anaerobic conditions during the wet season, and they bake hard and crack during the dry season. The texture of these soils also offers high resistance to root penetration. Furthermore, the pans are heavily grazed by plains game because the vegetation in these areas stays green for longer into the dry season than in the surrounding areas. These factors all combine to prevent the establishment of woody species. On the other hand, the presence and growth of woody vegetation in areas with relatively low levels of organic carbon, pH, water-holding capacity, and conductivity, which is associated with deep, sandy soils, is primarily limited by soil moisture. In general, woody vegetation with deeper root systems, as compared to grasses,

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are dependent on underground water during the dry season for survival (Shelton 1994). Often, sandy soils with their high permeabilities lead to a water table beyond the reach of all but the longest tap roots (Shelton 1994). This again leads to the exclusion of many woody species, including *A. mellifera*, from this habitat type. These factors can explain the presence of *A. mellifera*, and also most of the other larger woody species in the study area, in areas with intermediate levels of organic carbon, pH, water-holding capacity and conductivity, and soil textures types such as sandy-loam and sandy-clay.

It appears that rockiness is an important determinant influencing the presence and levels of *A. mellifera* in the study area. The association of *A. mellifera* with rocky areas is consistent with the findings of Bezuidenhout (1994) and Malan *et al.* (2001) who observed the same association. In the study area, these rocky habitats are often found on hill-slopes with shallow soil. In general, rock fragment content decreases the soil bulk density (Stewart *et al.* 1970; Cerda 2001) which would improve fine-textured soils such as sandy-loam or sandy-clay, thereby favouring the growth of woody vegetation (Poesen & Lavee 1994). In addition, rockiness protects the soil surface from sealing and crust formation by the impact of raindrops (Agassi & Levy 1991; Cerda 2001) and compaction (Poesen & Lavee 1994), thus increasing the water infiltration and percolation rates (Tromble 1976; Poesen *et al.* 1994; Poesen & Lavee 1994). This, and the reduced evaporation of water from the soil surface layers (Unger 1971) makes more water available in the deeper soil layers. In general, reduced evaporation therefore produces a more favourable environment for plant growth and especially for woody vegetation. The effects of rockiness on the temperature regime of the surface horizon of the soil is, however, not always positive (Poesen & Lavee 1994). As rock content or cover increases, thermal conductivity and heat storage capacity increases, especially in dry soils such as are found in semi-arid areas (Poesen & Lavee 1994). Rocky soils have been observed to warm more rapidly than rock-free soils, and during the hottest months of the year the temperature of these soils can become dangerously high, staying high for longer than non-rocky soils, affecting the physiological processes of some plants not well adapted to this type of environment (Poesen & Lavee 1994). Indeed, different relations between rock fragment content and soil and plant productivity have been observed for different plant species, i.e. negative, positive, ambivalent or no effect (Poesen & Lavee 1994). This might be because of differences in the supply and availability of water and nutrients in a specific soil, or a certain characteristic temperature regime and environment for plant growth, or due to differences in demand for these factors by different plant species.

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In some species, it was found that higher soil temperatures, as found in rocky soils, promoted early season growth (Fairbourn 1973). It might be that *A. mellifera* is one of these species with early seasonal growth giving it a competitive advantage over other species that are adversely affected by higher temperatures. Furthermore, in some cases it was found by Babalola & Lal (1977) that rock fragments in the soil had an inhibitory effect on root growth. This, and the likelihood that shallow soils are associated with rocky habitats in the study area, will rule out species with taproots or extensive and deep root systems. *A. mellifera*, however, has a very extensive lateral root system together with its tap root (Adams 1967), possibly making it less dependent on deep soil than other species. In arid and semi-arid areas, the relatively deeper penetration of the limited precipitation, and greater availability of water at low moisture contents in soils containing rock fragments in surface horizons, often results in these soils being more productive than comparable soils without rocks (Poesen & Lavee 1994). Poesen and Lavee (1994) observed that some shrubby deep-rooting plants seem to be better adapted to soils containing rock fragments than shallow-rooting grassy plants or trees. Kadmon *et al.* (1989) reported a positive effect of rock fragment content on the abundance of woody perennials in the northern Negev, Israel, and attributed this to the favourable effects of rock fragment content on water availability. *A. mellifera* might be a very good competitor with grasses for soil water in rocky areas. The higher availability of soil moisture in these areas than in non-rocky areas might provide ideal conditions for a woody species that is already adapted to the other effects of a rocky habitat – which can be assumed due to its preference for, among others, gravelly soil (Carr 1976; Smit 1999).

We therefore suggest that *A. mellifera* might naturally occur in high numbers in rocky areas because it seems to be a good competitor with grasses and even other woody species in these areas. This is supported by the lack of increase in percentage cover of this species in the rocky areas over time, suggesting a relatively stable state in the vegetative interactions in rocky areas within the time scale covered by the aerial photographs. *A. mellifera* does, however, seem to be encroaching in the non-rocky areas, and more so in recent years (1967-1993) than in earlier years (1957-1967).

It appears that grazing strategy does not have an effect on the presence and levels of *A. mellifera* in the study area. The low levels and lack of increase of *A. mellifera* in areas grazed/browsed by game can probably not be taken to mean that game grazing/browsing

prevents encroachment. Game was only introduced to the area they now occupy during the last 15 years, and this area was subject to the same grazing strategy before this time as the cattle area. Also, the increase in *A. mellifera* in the cattle area was due to increases after 1967, when grazing was carried out on a rotational basis and at a relatively low stocking rate. The fact that there was a difference in percentage cover of *A. mellifera* between the game and cattle/communal area as early as 1957 already indicates that another, unmeasured variable, is more important than grazing strategy in the determination of *A. mellifera* dynamics in the study area. The low levels of variability in the data which were explained by the CCA and the multiple linear regression, also indicates another, unmeasured variable is involved in the determination of *A. mellifera* dynamics in the study area. Effects of grazing strategy on the vegetation in the study area may be masked by the high inherent variability in rainfall and soil nutrients in semi-arid regions (Ward *et al.* 1999). Many authors have shown that stochastic variation in environmental variables, especially rainfall, may override or mask the impacts of herbivory on vegetation in semi-arid and arid regions (O'Connor 1985; Ellis & Swift 1988; Milchunas *et al.* 1989; Venter *et al.* 1989; Westoby *et al.* 1989; Behnke & Scoones 1993; Parsons *et al.* 1997), although this effect was not investigated over as long a time-period as that covered by the aerial photographs in this study.

6. Conclusion

The results obtained from this study support the hypothesis that bush encroachment is a natural phenomenon in semi-arid and arid environments, in systems such as savannas, which are governed by patch-dynamic processes (Wiegand *et al.* 2002). In these systems, the landscape consists of many patches in different states of transition between grassy and woody dominance. In the study area, rocky patches create an environment with increased water availability for tree germination and growth, improved soil structure for root penetration, and temperature regimes which might possibly favour woody growth more than grassy growth. These habitats are therefore likely to be more sensitive to heavy grazing and encroachment. Bush encroachment might also be seen as a "natural phenomenon" in the rocky areas in the study area, and at the landscape scale, this savanna system might be seen as stable. However, the increases in *A. mellifera* in the cattle/communal area and in the non-rocky habitats after 1967, might indicate a livestock induced increase in woody vegetation in the study area, and might be a cause for concern. The increase in *A. mellifera* after 1967, even though grazing

levels were lower at this time, suggests that the relationship between stocking rate and impact on the natural vegetation is not linear in nature, but that a threshold effect exists (Ward *et al.* 2000). The tree:grass ratio might remain stable at the landscape level, but as soon as the threshold level of utilisation is exceeded, the system might not be able to recover to the equilibrium it experienced before.

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Chapter 5

General conclusions and management recommendations

1. Background

Despite the fact that the South African savannas are well studied (Scholes 1997), and many industries in South Africa which contribute greatly to the country's economy (commercial cattle/game ranching, ecotourism and conservation) rely heavily on this ecosystem, the factors and processes involved in its functioning and dynamics, are still poorly understood. Specifically, factors involved in the determination of the tree:grass ratio within savannas are complex and the specific interactions between these are not clear (Ward 2002). In the study area, increases in the tree:grass ratio (i.e. bush encroachment by *Acacia mellifera*) are of specific concern due to the consequent reduction in the biodiversity and productivity of the area.

By investigating the effects of different management strategies (cattle, game, or communal ranching) and different soil characteristics on semi-arid savanna structure and function, we aimed to gain a better understanding of the functioning of these savannas in general. The role that management strategy and soil type play in bush encroachment dynamics were of further interest. The Kimberley Triangle, where different management strategies are practised on different soil types, but where bush encroachment is a common problem, was the ideal location for a relational study such as ours. In addition to its contribution to the general understanding of semi-arid savanna dynamics, we also believe that the results obtained from this study will contribute to one of the main objectives of the Kimberley Triangle development (see Chapter 1). This objective has been described as being "the stimulation of job creation, economic activity, and wealth creation through (here lies our focus), the optimal and sustainable use of the natural resource base (i.e. semi-arid savanna)" (Van Riet & Louw 1999). Below, we set out management recommendations, based on the findings of our study, which might prove to be helpful in the attainment of this objective, but also to individual land-owners, managers and ranchers in the study area.

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2. General conclusions

We have found that in the study area, and possibly in other semi-arid savannas under similar management types and on similar soil types, that the presence and availability of soil moisture and nutrients are more important in determining species composition than management strategy (see Chapter 3). This confirms current knowledge stating that soil moisture and nutrients are the main determinants of savanna, with herbivory (and fire, although this is not as important in semi-arid savannas due to low fuel loads) acting as modifying agents of the first two factors (Skarpe 1992; Teague & Smit 1992; Vetaas 1992; Solbrig et al. 1996 etc.). Our results are, however, contrary to the popular belief that heavy grazing is one of the main causes of bush encroachment in savannas (Walter 1954; Walker & Noy-Meir 1982). We found that soil moisture and nutrient content, which is generally reflected by the soil texture, soil pH, conductivity, water-holding capacity, and levels of organic matter in the soils of the study area, are more important than grazing in determining vegetation structure and composition, including the tree:grass ratio, both in the short (see Chapter 3) and long term (see Chapter 4). We found that the above-mentioned soil characteristics, indicating the presence and availability of soil moisture and nutrients, increased with the amount of clay in the soil. Furthermore, soil moisture limited the growth of woody species more than nutrient content did. The nutrient that is most important in the determination of tree-grass dynamics in the semi-arid savannas of South Africa, is nitrogen (Scholes & Walker 1993; Ward 2002). A large proportion of the woody component in the studied savanna consists of leguminous, N_2-fixing species (*Acacias*), which are therefore not limited by nitrogen deficiencies in the soil. This fact is important in the competitive interactions between the woody and herbaceous components in the system, seeing that N_2-fixing species will have a competitive advantage over non-N_2-fixing species in areas with nitrogen deficiencies, as found in, for example, the sandy areas in the study area. Yet, the occurrence of woody species was limited by soil moisture in these areas. Rockiness, however, ameliorates this condition through increased infiltration of water into the soil, and high levels of woody vegetation are often found in such rocky areas.

In the light of the above factors, we suggest that sandy habitats are relatively resistant to increases in woody vegetation (including N_2-fixing species) due to its low potential water presence and availability, which limits woody growth. Clay soils and the clay-pan habitats

are also resistant to invasion by N_2-fixing woody species which are out-competed by the herbaceous component which is not limited by nutrients and which are better competitors for soil moisture than woody species in these habitats. Additionally, the fine soil texture found in these areas impedes root penetration and the seasonal water regimes found in the clay-pan habitats further impedes the establishment and survival of woody species in these areas, making it more resistant to encroachment. On the other hand, in areas with intermediate levels of sand/clay (loamy-sand, sandy-loam, sandy-clay-loam and sandy-clay), N_2-fixing woody growth is not limited by soil texture, moisture, or nutrients, and the removal of the suppressive, competitive effect of the grass layer on the woody layer due to heavy utilisation, can easily lead to encroachment in these areas. Where *A. mellifera* is concerned, rocky habitats seems to be especially sensitive to encroachment. However, results obtained from the aerial photograph analyses suggested that *A. mellifera* might naturally occur in high numbers in these areas, because it seems to be a good competitor with grasses and even other woody species in these areas with higher levels of soil moisture. The above results all support the patch-dynamic approach (Skarpe 1992; Scholes & Archer 1997; Illius & O'Connor 1999) to savanna processes. The savannas in the study area can therefore be seen as consisting of many patches (i.e. sand, clay, and rocky patches, and different combinations of these) in different states of transition between grassy and woody dominance (see Chapter 4 for details).

The relatively greater importance of soil type, through its effects on soil moisture and nutrients, on vegetation than management strategy can not be taken to mean that stocking rate or management strategy are unimportant as factors determining savanna structure and tree:grass ratio. Indeed, we found that of the management strategies studied, communal utilisation, with its associated heavy and continuous stocking rates, had the greatest potential to cause degradation of the natural vegetation. We do, however, suspect that a non-linear relationship between stocking rate and impact on soil and vegetation exists, meaning that degradation and consequent reduction in the productivity of the natural vegetation will mainly occur once a certain threshold of utilisation has been reached. The aerial photograph analyses were useful in the investigation of long-term trends in bush encroachment. We found an increase in *A. mellifera* in the study area that is not related to the natural presence of this species in the rocky areas. The cause of this increase remains unclear and management strategy did not seem to be the cause of this trend. It is nonetheless a matter of concern, since it indicates a general trend of long-term vegetation degradation in the study area.

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3. Management recommendations

Given the threshold effect of vegetation degradation and bush encroachment in the study area, as well as the relative resistance of certain habitat/soil texture types to encroachment, ranch production might be economically maintained/increased if stocking rates are increased on the sandy and clay habitats for a number of years. By this we do not suggest over-utilisation for maximum economic profit in the short-term, but a balance between the economical and ecological viewpoints of sustainability need to be found where the increased income in the short-term must be measured against the lower productivity linked to increased woody vegetation and the costs involved in managing the problem in the long-term. The introduction of additional browsers, e.g. certain game species, might be a relatively safe way to increase economical productivity without running the same level of risk of degradation of the natural vegetation in the long-term as would be the case when only cattle numbers are increased in an area. Browsers are often believed to control the recruitment of woody species to the adult, fire-resistant stage where they cannot be out-competed by the herbaceous component (Trollope 1980; Scholes & Walker 1993), although we found no evidence of this. Species such as kudu (*Tragelaphus strepsiceros*) and giraffe (*Giraffa camelopardalis*) are classified as preferential browsers. Although kudu naturally occur at low densities, this species has the advantage of not competing with cattle in terms of vegetation utilisation as it is almost exclusively a browser (Fritz et al. 1996). Owen-Smith & Cooper (1985) also suggested that the reason for the low densities in which kudu naturally occur is due to the fact that a large proportion of the browse that this species relies on is out of reach, and if leaves fall to the ground, they become too dispersed to be efficiently ingested. They suggested that stocking densities of kudu can be increased by setting out suitable collection baskets under deciduous trees, thus making additional feed available to kudu *in situ*, reducing the need to buy supplementary feed. Giraffe, on the other hand, are not limited by browse being too high to reach. We suggest that *Acacia erioloba* parkland vegetation is ideal for introduction of this species. Additionally, mixed feeders such as springbok (*Antidorcas marsupialis*) and other plains game (e.g. black wildebeest (*Connochaetes gnou*)) preferentially utilise the encroachment resistant clay-pan habitats, making this an important habitat to increase, or at least diversify utilisation of an area. It must, however, be kept in mind that the numbers of grazers in an area might have to be reduced in certain seasons of the year if additional

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browsers are introduced, seeing that few species are exclusive browsers and most do graze at certain times of the year.

Although the probability of encroachment should be lower in the sandy and clay habitats, other general forms of land degradation, e.g. increases in unpalatable/poison plants, early successional species with usually low nutritive value, or reduced cover of vegetation, can still occur in heavily utilised areas. This is indeed the case in the communal part of the study area. Undesirable species include: Vermeerbos (*Geigeria filifolia*), Januariebos (*Gnidia polycephala*), Slangkop (*Ornithoglossum undulatum*), and Bitterbos (*Chrysocoma ciliata*), which are all poisonous to some degree and often indicate heavily utilised vegetation. The common occurrence of the grass species *Eragrostis obtusa*, *Aristida congesta* and other *Aristida* species, in an area is often an indication of heavy grazing. Additionally, these species are of low value as grazing species due to low leaf production and their fibrous nature which causes low digestibility (van Oudshoorn 1994). All these species occur in the study area and any increases in these can be taken to mean that vegetation degradation is occurring or progressing in an area and can be used by managers to monitor, in a simple way, the state of the system.

The areas with intermediate levels of clay in the soil (loamy-sand, sandy-loam, sandy-clay-loam and sandy-clay) should be utilised conservatively, due to their sensitivity to encroachment. In these, and also specifically rocky areas (generally > 15 % rock on the surface) utilisation levels that lead to a grass layer with reduced productivity and competitiveness should be avoided. Seeing that cattle often avoid rocky areas if given a choice, we suggest that game species (grazer/browser mix), which are not prohibited by rocks, or prefer rocky habitats, are introduced to these areas. This will lead to a more even utilisation of the grassy and woody components, reducing the probability of the grass layer being over-utilised and the woody layer being under-utilised, a situation which could lead to bush encroachment.

In general, because moisture limitation is such an important variable determining woody plant abundance in the study area, we suggest that heavy grazing in above-average rainfall years should be limited in all habitats. N_2-fixing species, which are more limited by soil moisture than nutrients, will have the opportunity to germinate *en masse* in years when moisture is not limiting, and if grasses are removed by heavy grazing during these times, N_2-fixers would be

able to establish and reach a stage at which grasses will not be able to out-compete them, and encroachment may occur.
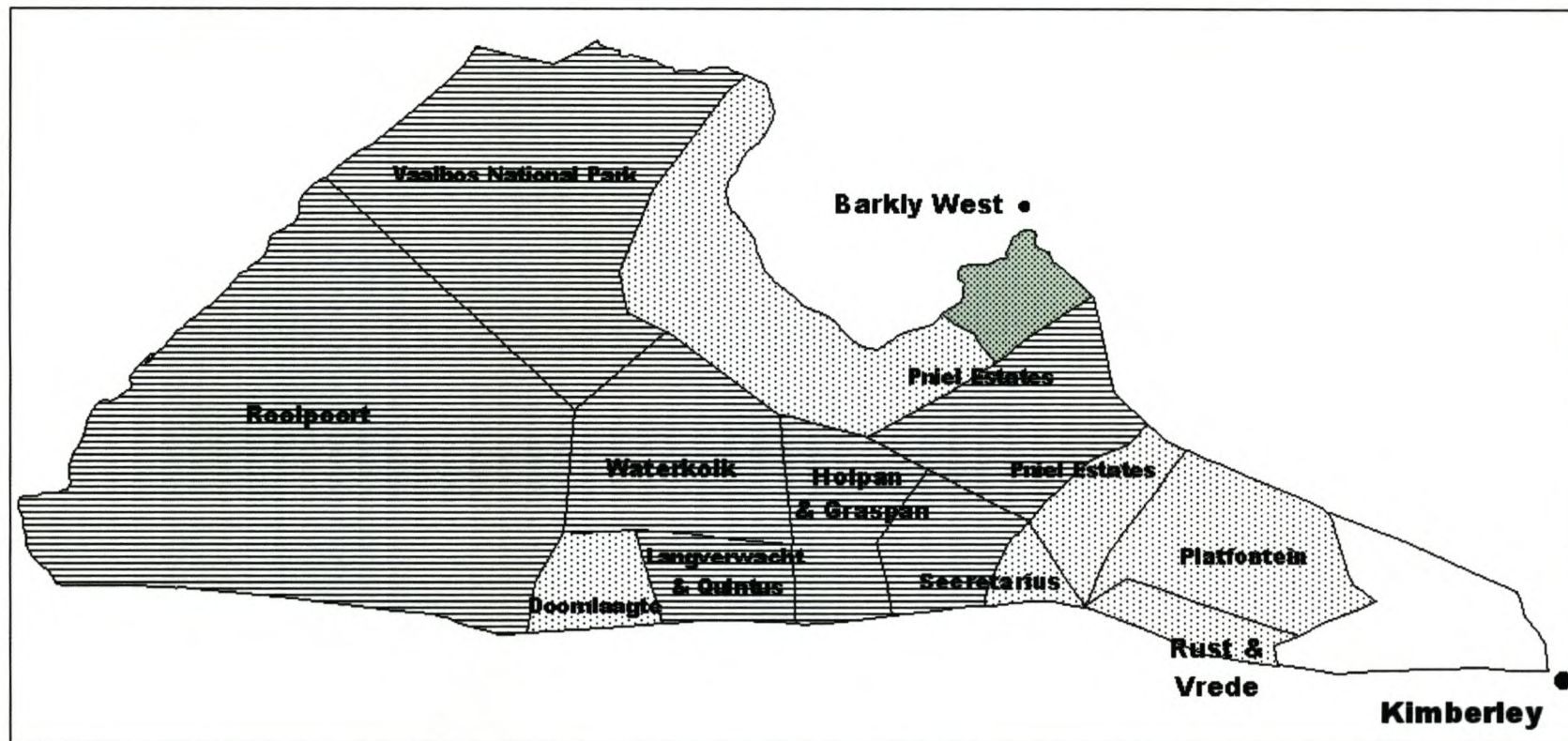
4. Tools to assist land managers

In order to apply the above management recommendations, managers need to be able to determine at least one soil characteristic such as soil texture, which is indicative of the general sensitivity of an area to bush encroachment. Although soil texture can be determined relatively simply, rapidly, and on location in the field, using finger-texturing methods, some level of previous experience is needed to obtain a standard level of accuracy. Other soil characteristics such as the organic matter content (measured as percentage organic carbon), or soil pH can, however, be used as an indication of soil texture, being positively correlated with the percentage clay particles in the soil (see Chapter 3). Organic matter content can be used as a direct indication of potential soil moisture and nutrient contents as it influences a soil's water-holding capacity and cation-exchange capacity positively (see Chapter 2). The determination of these factors (organic carbon and soil pH) can be determined at a reasonable cost by any professional soil testing laboratory. Additionally, Figures 5-2, 5-3 and 5-4 can be used as a general indication of the distribution of soil texture, soil organic carbon and soil pH in the study area respectively. Note that soil texture (Figure 5-2) provides the most detailed information on soil conditions in the study area. When the other two variables, organic carbon (Figure 5-3) and soil pH (Figure 5-4), are used in management planning, it should be done conservatively. [Note: these maps were generated by collecting soil samples from the study area in a stratified random manner (stratified according to management strategy). Coordinates of each sample were noted and this fact as well as the soil characteristics obtained by soil analyses was used to create these maps through interpolation using ArcViwe 3.2 software].

We also found aerial photographs to be useful in determining long-term trends in the vegetation of the study area. Unfortunately, the technology to accurately analyse these is not always readily available/accessible to land-managers. Long-term trends in vegetation can, however, still be investigated by making use of fixed-point photography (see Rhode (1997) for a detailed description of the method). This method employs the comparison of photographs, taken of exactly the same landscape, over a number of years. If the photographs

are of an acceptable quality (i.e. containing details relevant to the question being asked), they can be an accurate tool to track vegetation changes of a specific area over a number of years. If information on factors such as management strategy, rainfall etc., are recorded along with the photographs, this information can possibly be related to any noticeable changes in the vegetation. In such a way, managers can see the direct effect of the management strategies employed, or environmental conditions that exists/existed in an area, and adapt their management accordingly.

If archival photographs are available, they can be incorporated into a time series of photographs of an area. The specific location from whence these were taken needs to be established, though, in order for the time series to be continued. This can quite accurately be determined through triangulation (Rhode 1997) if at least two easily recognisable features are present on the photo e.g. a tree, building structure, dam, road. If archival photographs are not available, a new time series can be initiated. It is strongly recommended that the point from which photographs are taken is marked in the landscape in a permanent manner e.g. by a heap of stones or a pole. All subsequent photographs must be taken from exactly this point in order to make photographs comparable between years. Also, care must be taken to include the same view of the landscape in all photographs. Furthermore, photographs must be taken during the same season of the year, and if possible, the same time of day, as this can influence the shadowing of the picture, and thus interpretation. All photographs must also be labelled in a permanent manner with information such as date, time, location, etc., to avoid later confusion. If information on environmental or management factors is also noted, this must also be added.

It is clear that our semi-arid savannas are complex systems, consisting of a patchwork of different habitats, each with a different resilience and stability. Therefore, the ideal would be for these patches to be managed individually to ensure maximum long-term productivity and stability. Indeed, biological complexity and diversity are essential components in the sustainability of semi-arid savanna rangelands. A diversification in the utilisation of the vegetation by grazers, browsers, and mixed feeders is important in maintaining this diverse system and may additionally, to some extent, reduce the risks run in monospecific ranching strategies by being able to cope with climatic uncertainties, e.g. droughts.

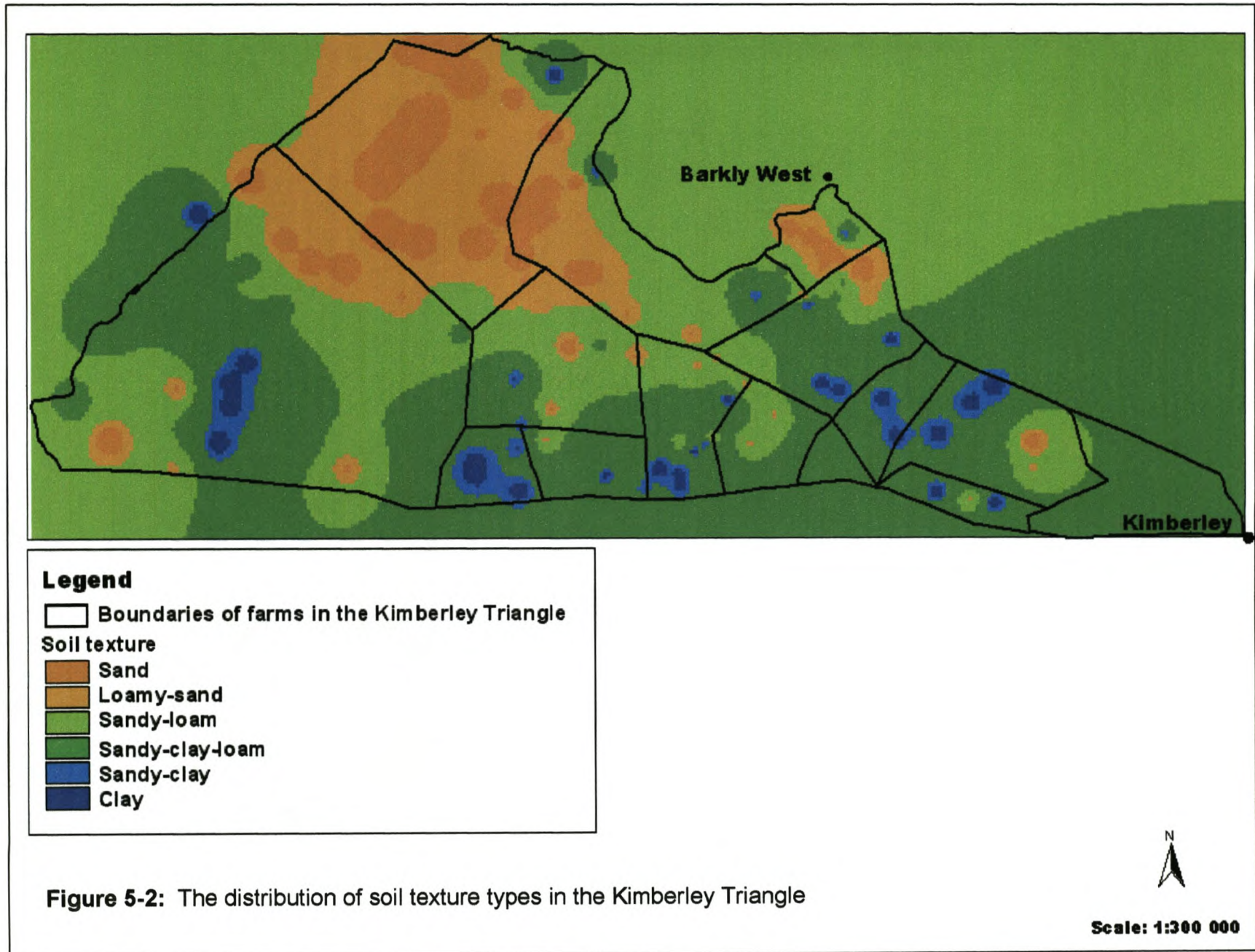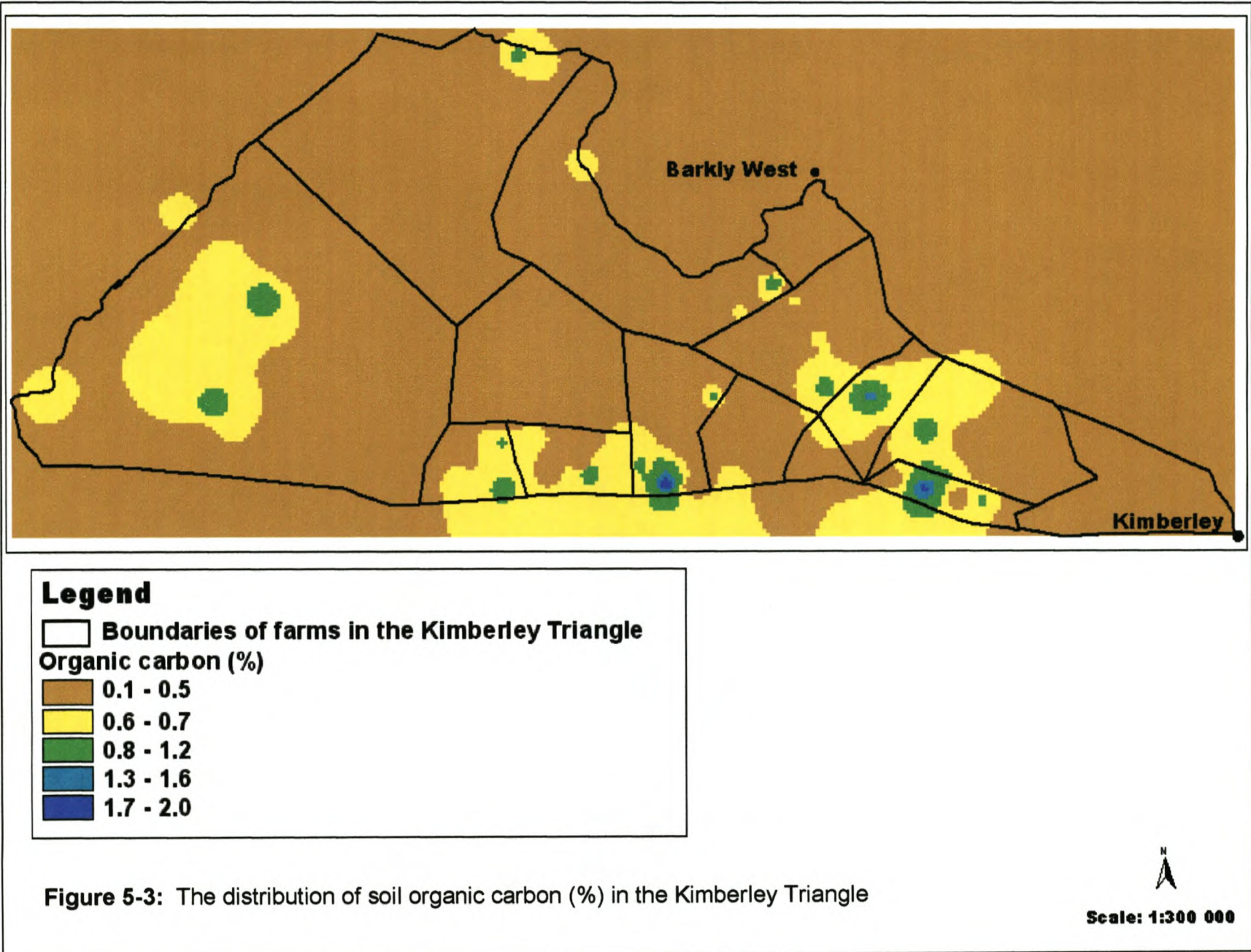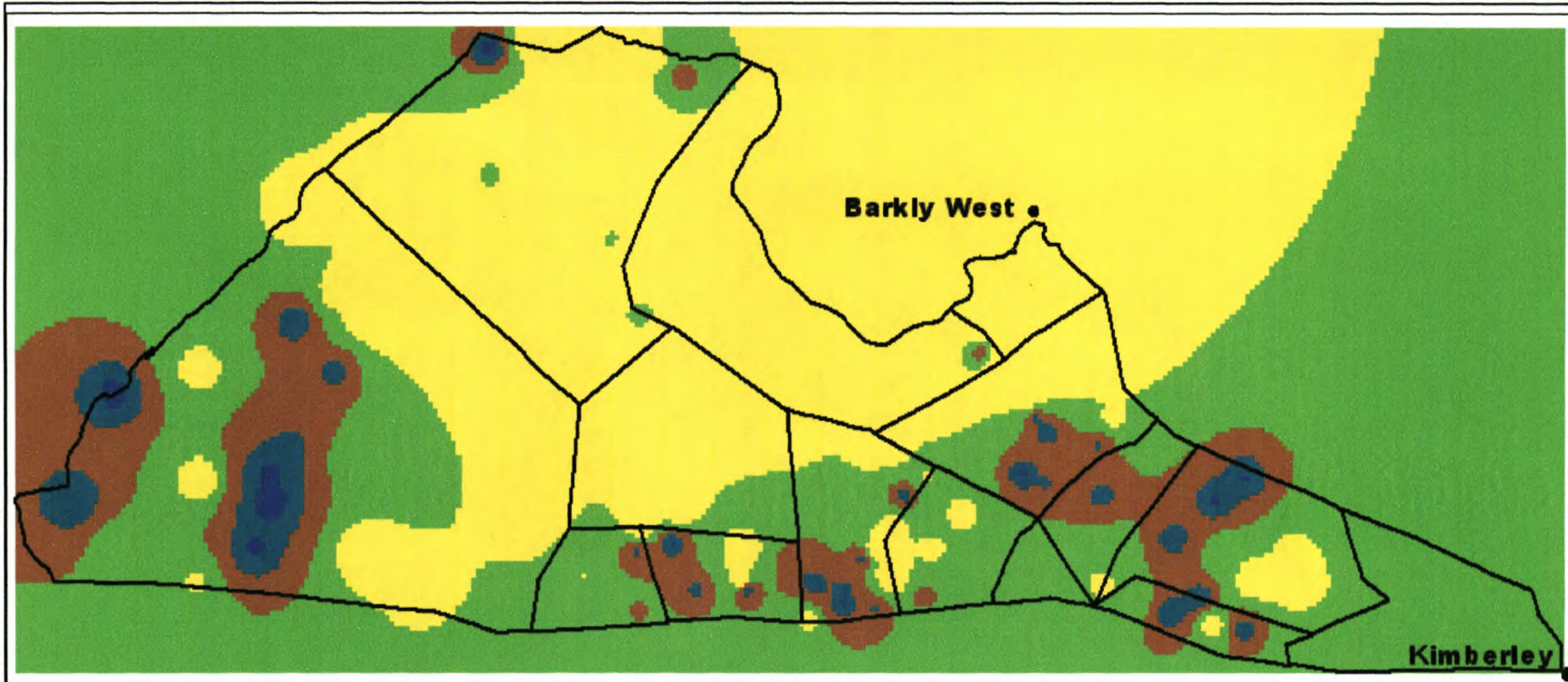**Figure 5-1:** The Kimberley Triangle with different management strategies

Scale: 1:300 000

Legend

☐ **Boundaries of farms in the Kimberley Triangle**

Soil texture

- Sand
- Loamy-sand
- Sandy-loam
- Sandy-clay-loam
- Sandy-clay
- Clay

Figure 5-2: The distribution of soil texture types in the Kimberley Triangle

Scale: 1:300 000

Legend

Boundaries of farms in the Kimberley Triangle

Organic carbon (%)

■	0.1 - 0.5
■	0.6 - 0.7
■	0.8 - 1.2
■	1.3 - 1.6
■	1.7 - 2.0

Figure 5-3: The distribution of soil organic carbon (%) in the Kimberley Triangle

Scale: 1:300 000

Legend

☐ **Boundaries of farms in the Kimberley Triangle**

Soil pH

- ☐ 4.3 - 5.6
- ☐ 5.7 - 6.2
- ☐ 6.3 - 6.9
- ☐ 7.0 - 7.5
- ☐ 7.6 - 8.2

Figure 5-4: The distribution of soil pH levels in the Kimberley Triangle

Scale: 1:300 000

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