Towards a predictive understanding of savanna vegetation dynamics in the eastern Lowveld of South Africa: with implications for effective management

by

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DECLARATION

The experimental work described in this thesis was conducted in the eastern Lowveld savannas of the Limpopo and Mpumalanga Provinces, South Africa from 1990 to November 2005, under the supervision of Professor P J K Zacharias and Dr H C Biggs.

These studies represent the author's original work, unless specifically acknowledged and stated in the text, and have not otherwise been submitted in any form for any degree or diploma to any University.

M.J.S. PEEL

Professor P J K Zacharias (Supervisor)

Dr H C Biggs (Co-supervisor)

DECLARATION ON COPYRIGHT

The work reported in this thesis is based on published work as follows:

Chapter 2: Published as: M.J.S. Peel, R. Davies and R. Hurt. Chapter 28 (2004) In: Indigenous Forests and Woodlands in South Africa - policy, people and practice. M.J. Lawes, H.A.C. Eeley, C.M. Shackleton and B.G.S. Geach (Editors). University of KwaZulu-Natal Press, pp 775-795. (Appendix 1a).

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ABSTRACT

The purpose of this study was to develop and test a predictive understanding of the vegetation dynamics of the Lowveld of South Africa (30°35'E to 30°40'E and 24°00'S to 25°00'S). The study covered about 5000 km^2 in Adjacent Private Protected Areas (APPA) adjoining the Kruger National Park (KNP).

Data gathering (800 sites; 23 properties) commenced in 1989 and those recorded up to 2004 are reported here.

The value, both ecological and economic, of the wildlife and tourism industry dependent on this savanna region is discussed in both historical and current perspectives. A range of land-use objectives and anthropogenic interventions were exposed. The properties ranged in size from 30 to 800 km^2 and formed an effective and extensive manipulative experiment for investigating interaction of bush density, animal stocking, use of fire and landscape-scale processes. The first descriptive classification (at 1:250 000) of the area was developed using Inverse Distance Weighted interpolations. This confirms similar landscape/vegetation patterns in the KNP and Mocambique.

The current mode of determining stocking density or carrying capacity was interrogated and indices suitable for complex multi-species systems developed. This was done in the context of equilibrial/disequilibrial paradigms. Application of the original indices resulted in drought-related declines in animal biomass of 4000 kg km^{-2} over 20 years due to overestimation of carrying capacity. The model proposed here uses rainfall, animal type, biomass and vegetation parameters to determine stocking density for both coarse- (regional) and ranch-specific scales.

Principal driving determinants (rainfall, geology, soil type, tree density canopy cover, animal numbers, feeding classes and fire) of vegetation structure and their influence on the herbaceous layer were investigated. Groupings on ecological potential showed ‘high’ potential areas are less sensitive to animal impact than those classified as ‘low’ potential.

Sustainability, embedded in a forward-looking component viz. Strategic Adaptive Management (SAM) with well-articulated endpoints viz. Thresholds of Potential Concern (TPCs) was used to study fluctuations in animal populations with *Connochaetes taurinus* (Blue wildebeest) as the case study.

The TPC approach provides strong pointers for proactive management aimed at maintaining the system within bands defined by TPCs supporting operationally practical and periodically reviewed objectives.

For Clotilde, Dominique and Nicholas

Your support and love is appreciated more than you will ever know

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Chapter 1

A context for the study

The Savanna Biome comprises some 35% of the land surface of South Africa in southern Africa (Scholes & Walker 1993). The study area, situated entirely in the Savanna Biome (as classified by White (1980)), is located in the eastern Lowveld (EL) of South Africa, to the east of the Drakensberg escarpment, between 30°35'E and 30°40'E and 24°00'S and 25°00'S. The area is further classified as a semi-arid savanna, exhibiting a strong correlation between annual primary production and annual rainfall (Rutherford & Westfall 1986). The semi-arid savannas described in this study are divided into dystrophic (moist and leached) and eutrophic (dry and more fertile) elements.

The Savanna Biome is home to most of the human population in Africa and contributes significantly to primary production and the organic carbon pool, a factor that will become increasingly important in the future. The savanna is thus important to the livestock and wildlife industries in this region, and ecological research must strive to gain an understanding of its functioning in order to provide sound management guidelines.

O'Connor (1985) provides a synthesis of experiments concerning the grass layer in the savanna regions of southern Africa. This synthesis reports that the order of variables, based on the number and duration of experiments, was herbaceous composition, total basal cover, yield, soil properties and soil density. There is, however, a paucity of medium- to long-term (greater than five years) experiments (O'Connor 1985) nor are there long-term data sets monitoring any system's responses readily available. This situation has not changed appreciably since his review over two decades ago!

The relation between water and nutrient availability (soil related), competition between plants for resources, and plant production and quality influences patterns of herbivory and fire, and are therefore critical in understanding savanna dynamics (Frost *et al.* 1986). Rainfall, soil, herbivory and fire, working singly or in combination, create a spatially and temporally shifting mosaic of challenges and opportunities to plants which result in different species compositions, abundance, cover and utilisation patterns (Figure 1).

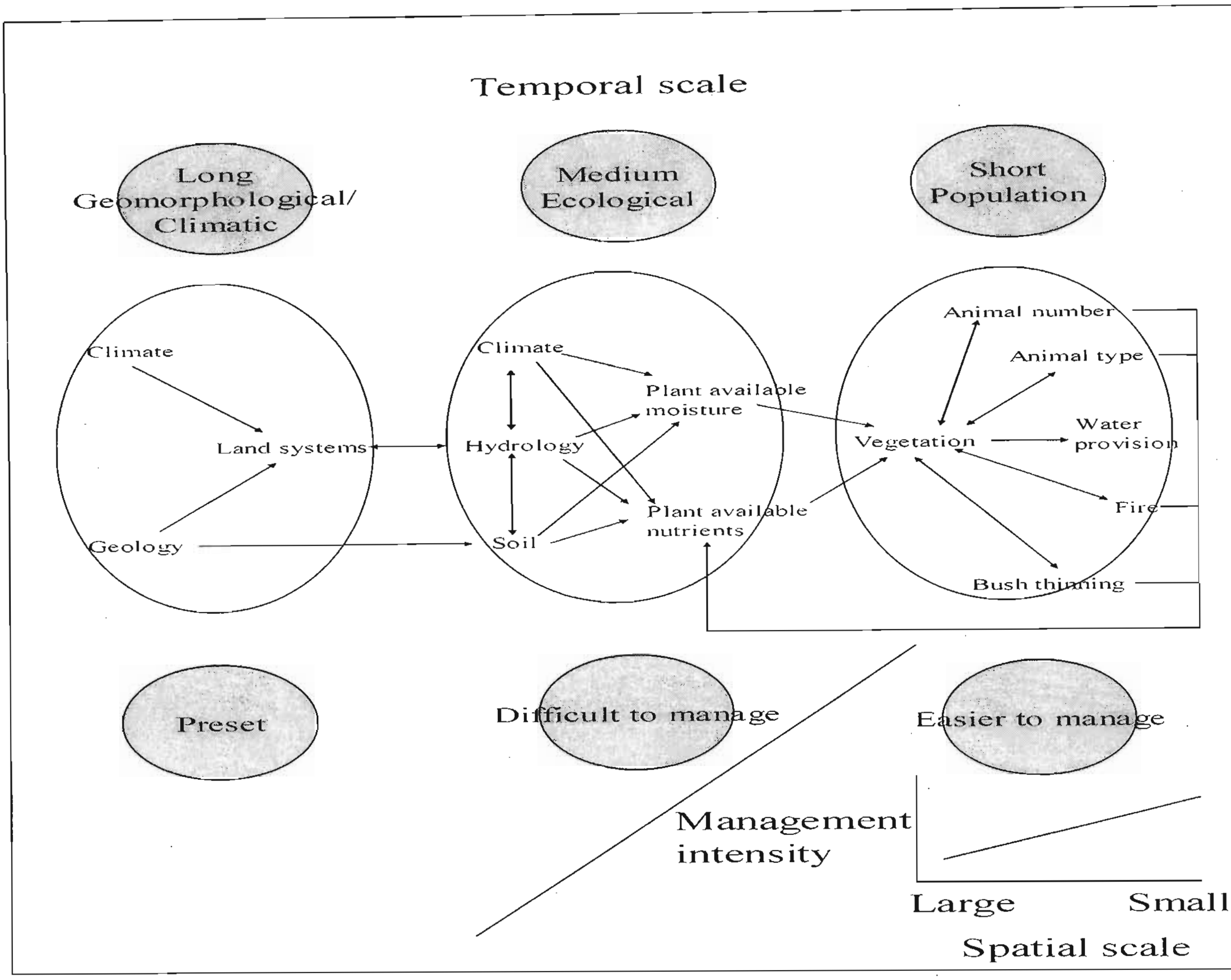

Figure 1 Interactions of the major driving determinants of southern African savannas (modified after Walker 1984).

The need for this study is occasioned by the dramatic increase in land area under private conservation management and its potential to contribute to global objectives by maintaining biodiversity through sustainable management (e.g. van der Waal & Dekker 2000). Furthermore, the wildlife industry and its associated tourism activities form a significant component of the economy of the region.

The aim of the study was **to investigate the potential of the natural resources of the Lowveld to contribute to the economy and development of the region.**

The two broad objectives of the study can be summarised as follows: **to gain a predictive understanding of savanna vegetation dynamics in the Lowveld of the**

Mpumalanga and Limpopo Provinces, and using knowledge thus gained, to incorporate results obtained into the effective management of these and related savannas.

Key questions

The objectives are translated into the following goals that define this thesis:

1. to better understand the determinants and processes of primary production in the savannas of the Lowveld; and
2. to better understand the relative importance of environmental drivers (in particular soil and rainfall parameters) and management modifiers (in particular animal number and type) and the processes and mechanisms of primary production at different spatial scales. This will allow a better understanding of the relative ecological potential of different areas (at a landscape scale); and
3. to better understand the roles of system modifiers over which management has control including variables such as herbivory, fire and the control of bush density, on vegetation composition and structure.

I set up over 800 vegetation sampling sites on a number of discrete units covering an area of 5000 km^2 roughly between the Sabie River and Selati River adjacent to the western boundary of the Kruger National Park (KNP) starting in 1989. I refer to the area as the Adjacent Private Protected Areas (APPA). An ongoing ecological monitoring programme is in place where a subset of the abovementioned sites (between 510 and 560) has been monitored annually to detect change over time. The database also includes data on the environmental and management interventions. These discrete units are invaluable when assessing the effects of different management regimes on the vegetation in a savanna region with relatively low and, prospective increasingly variable rainfall (Venter *et al.* 2003). In effect the APPAs provided a massive manipulation experiment to investigate the impact of a range of management interventions.

This extensive database has been used to provide a framework for user-friendly decision support systems for the land user (e.g. Peel *et al.* 2002). Generic models describing a range of different ecological states of the resource have been constructed that can be translated into management actions that are aligned to landowner objectives (Chapters 4 through 6). The purpose of this thesis is to report on these developments.

Structure of the thesis

The current goals for each chapter are:

1. In Chapter 2, I outline the history of wildlife conservation and the development of the wildlife industry in the eastern Lowveld. With the significant change to wildlife utilization in areas to the west of the central section of the Kruger National Park there is a critical need to provide sound information. This is particularly important when we consider that most of the research work previously done was aimed at preservation strategies, focusing mostly on individual species of mammals, with little information on the sustainable use of the wildlife on small and intermediate estates, many of which are fenced. Woody densities have increased in many Lowveld areas with a concomitant reduction of the grass layer. This prompted a synthesis of the causes of and problems associated with this phenomenon. I go on to examine the economic costs and ecological implications of bush control which is practised on every property in the current study using a number of different management scenarios with differing primary objectives and based on actual case studies. This chapter provides a comprehensive review of the processes that have shaped the ecosystem in the study area and includes an economic analysis that, in combination justifies wildlife as a sustainable form of land use. The question of the impact of elephants is not covered here as the debate, both political and scientific (Cumming 2005; Grant 2005; Scholes *et al.* 2003; Whyte *et al.* 2003), post dates this published work (Chapter 2). This issue is now under controlled review through an extensive exclosure-based experiment in the KNP (SANParks 2001);
2. In Chapter 2 wildlife utilisation is justified as an ecologically and potentially economically viable form of land use. The phytosociological classification provided in this chapter contributes to recognition of the fact that different parts

of the study area have different ecological potential. This in turn has important implications for the setting of realistic objectives in these areas. Fenced areas, managed in isolation (dominated by management interventions), provide empirical observations from which to deduce critical thresholds of interaction among components and give us insights into the relevance of ecological scaling. Chapter 3 therefore aims at detecting pattern and defining its spatial scale in a manner that is meaningful to management. Management at local scales has, in turn, a potentially critical impact at both regional and global scales, the direct effect of changing the degree of interaction among patches altering system behaviour and ultimately influencing higher level processes;

3. Having provided context for the study in Chapter 2 and a description of the bio-geophysical template on which the ecosystem functions in Chapter 3, it was necessary to define some indices based on two critical drivers of the system viz., animal number and type. The latter has been little discussed despite the multi-species situation in which we find ourselves in southern Africa. Methods of determining animal densities (stocking rate) based on metabolic mass, animal type and biomass are reviewed in the context of equilibrial/disequlibrial paradigms. Equilibrium theory assumes a sufficiently homogenous system with a supposed optimal point of stability with non-deterioration of vegetation or soil over an extended term (Danckwerts 1982a; Trollope *et al.* 1990). On the other hand, two of the central tenets of disequilibrium theory are that there is no central tendency (point of equilibrium) and that plant and animal dynamics are uncoupled (Behnke *et al.* 1993). In South Africa, the calculation of 'carrying capacity' is based on conversion of animal species to metabolic mass equivalents. This assumes homogenous systems that tend to some point of equilibrium. It is applied widely in commercial livestock systems involving one or two species. In Chapter 4 I therefore examine these issues using a case study and present an approach to determine stocking density using animal type, biomass, rainfall and vegetation parameters;

4. Having provided a comprehensive context for the study, I now address the need to effectively manage these savannas. In order to do this, we need to understand the

forces that drive them. In Chapter 5 what we consider the principle driving determinants of these savannas were grouped to establish their influence on the limiting herbaceous layer (Figure 1; Walker 1984; Scholes & Walker 1993). Grass type, abundance and cover were examined in order to group areas of similar ecological potential. The results have implications for land users and policy makers in terms of setting guidelines for animal stocking density;

5. I have assessed the ecological potential and current condition of an extensive savanna at landscape (1:250 000) scale, and looked at critical response variables under similar environmental and woody vegetation conditions but with different management regimes and operating at different spatial scales. In Chapter 6 I look at this within the context of biogeophysical sustainability, examining the concept of thresholds and thermodynamics. The so-called 'sustainability' approach allowed for the construction of systematic contexts describing the ability or inability of a system to provide goods and services and achievement of land user objectives. This approach is a unique contribution to wildlife utilisation in these savanna areas;
6. To provide a novel approach to natural resource management in particular in varying size areas that have been re-scaled through management interventions. Re-scaling occurs for example when management provides water in seasonally waterless areas. The result is that animals, instead of following traditional migratory routes, become sedentary resulting in altered temporal and spatial utilisation patterns, and ultimately altered system functioning;
7. Elements that should be included in decision support systems for the land user are presented within a scientific framework. This brings into consideration the setting of realistic goals and objectives for a piece of land. Monitoring of important variables is ongoing and allows for refinement of models using data thus obtained. The result will be a flexible (adaptive) management style in which hazards are avoided and opportunities grasped (*sensu* Westoby *et al.* 1984), to the benefit of the reserve. The primary purpose of which is to be proactive rather than reactive.

Note to reader: The style and format of this document together with the bibliographic details for each chapter vary according to the requirements of the journal to which the work was submitted or has been published (Appendix 1).

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Chapter 2

The value and costs of wildlife and wildlife-based activities in the eastern Lowveld savanna, South Africa

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Introduction

Humans have been associated with Africa for more than two million years as hunters, pastoralists and cultivators, an association that has had a profound effect on the structure and extent of the savanna biome (Harris 1980). Early European travellers described the sub-continent as an area inhabited by large numbers of a wide variety of wild herbivores (Grossman et al. 1999). There is, however, some conjecture as to the reliability of many of these anecdotes as early travellers were dependent on water for their livestock, which would have brought them into contact with higher concentrations of wild herbivores than elsewhere (Liversidge 1978; Grossman et al. 1999). This aside, the last half of the nineteenth century is known worldwide as the 'century of extermination' (Carruthers & Pienaar 1990). European settlers and their livestock moved into the interior of countries such as South Africa and effected large-scale reductions in the numbers of indigenous wild herbivores. The rinderpest epidemic of the 1890s further diminished herbivore numbers in South Africa. Mercifully, the 'century of extermination' was followed by the 'century of conservation' (Carruthers & Pienaar 1990). Concerted efforts during the twentieth century have resulted in an increase in the number of wild herbivores to levels where non-consumptive use is possible, and even to the point where consumptive use is necessary.

South Africa's wildlife commands a high value both regionally and globally. However, this value is often ignored because it is difficult to quantify and the depletion of wildlife and natural resources is not generally seen as an economic cost to society (Davies 1997). The value of wildlife is not fully represented in economic decisions and wildlife-based activities are often viewed as being less profitable than activities that generate more easily quantifiable benefits and outputs to society. By demonstrating wildlife values and expressing them in monetary terms, wildlife is placed on an equal footing with other sectors of the economy. This provides important information for justifying and financing wildlife conservation, for using wildlife as a means of economic development and for setting in place economic activities that promote sustainable resource use.

Given its proximity to the world-renowned Kruger National Park and the wide variety of wild herbivores it supports, the eastern Lowveld region of Limpopo Province has attracted much attention, particularly in terms of wildlife-based tourism activities. Prior to the erection of a fence along the western boundary of the Kruger National Park in the 1960s and the sub-division of land to the west of the park, there was a large-scale east-west seasonal migration of herbivores from the western part of what is now the Kruger National Park towards the Drakensberg mountains. At this time, fire was probably important in maintaining the wooded grassland savanna, with a continuous herbaceous cover of mainly heliophilous C4 grasses and sedges and a woody component of mature trees and shrubs (Frost et al. 1986; Trollope 1992). The erection of boundary fences necessitated the provision of water in previously seasonally waterless areas. This in turn led to increased grazing pressure which, with a concomitant reduction in the frequency of hot fires, ultimately promoted bush thickening or encroachment (see below). Wildlife-based tourist operations in the region are adversely affected by such bush encroachment because the dense woody layer reduces game visibility. Consequently, bush control, which has important implications for the economic viability of wildlife operations, is practised on all of the protected areas included in this study (Peel 2002a).

Communal rangelands surrounding these wildlife areas are also under severe pressure from a growing population, through clearing of bush for fuel and carving wood as well as for agriculture. In addition to traditional bush-clearing techniques, sophisticated modern methods have allowed people to rapidly change the composition, density and structure of savannas through chemical and mechanical means. It is now more critical than ever that the needs of people are met without a decline in the long-term sustainability of natural resources. Alternative models of development, whereby communities surrounding wildlife areas benefit both socially and economically without causing a decline in the sustainability and productivity of the system, are urgently needed.

In this chapter, we outline the history of wildlife conservation and the development of the wildlife industry in the eastern Lowveld. This is followed by a synthesis of the causes of and problems associated with bush encroachment. We go on to examine the economic costs and ecological implications of bush control using a number of different management scenarios with differing primary objectives and based on actual case studies.

The history of wildlife conservation and game ranching in the eastern Lowveld

In examining the current status of woodland in the eastern Lowveld it is useful to investigate the factors that have shaped these savannas over the past two centuries. Until the beginning of the nineteenth century, life appears to have been relatively harmonious in the eastern Lowveld. This changed with the coming to power of the Zulu King Shaka to the south of the region, with ripple effects being felt throughout southern Africa as people fled his dictatorship (Eloff 1990). Manukosi, who broke away from Shaka, practised a scorched earth policy as he and his followers moved through the Lowveld region. When he died, his sons began to fight and every winter until the early 1860s the eastern Lowveld as far as the Olifants River was ravaged by fire. Large-scale anthropogenic fires have thus occurred in the region as far back as 130 years ago, if not longer.

As early as 1884, President Kruger expressed concern at the levels of game hunting in the eastern Lowveld and advised the setting aside of some land to ensure the continued survival of wild animals in the area (Stevenson-Hamilton 1937). The notice proclaiming the Sabi Game Reserve was gazetted in 1898. In the 1890s, W.H. Gillfillan, who later became first surveyor-general of the Union of South Africa, surveyed the area adjacent to the Sabi Game Reserve between the escarpment and the Lebombo mountains and between the Sabie and Olifants Rivers into 4000 morgen (3428 ha) lots (Stevenson-Hamilton 1929; Porter 1970; Bornman 1995). These were sold, first to ranchers and then to mining companies who thought the area might be rich in minerals. In 1903 the protected area of the Sabi Game Reserve was extended north to the Limpopo River and in 1926 the National Parks Bill was passed, which paved the way for the proclamation of the Kruger National Park (Stevenson-Hamilton 1929).

In 1923 the Secretary of Lands announced that the Sabi Game Reserve would be cut up into farms and large land companies began cattle ranching in these protected areas (Porter 1970). This continued until a compromise was reached and an area on the western border was given to the Land Estates Companies in exchange for the portion of land between the Olifants and Letaba Rivers (Porter 1970). From 1922 the Transvaal Consolidated Land and Exploration Company (TCL) ran large-scale cattle operations in much of what is now the Sabi Sand Wildtuin, buying large tracts of land for between 12 and 74 shillings per hectare (Toulon in the Sabi Sand Wildtuin was bought for 30 pounds in 1884) (Kloppers 1970). In the winter of 1928 two rangers were appointed by Harry Kirkman to combat poaching in the western and northern parts of the Sabi Sand Wildtuin (Kloppers 1970). This was the beginning of organised game conservation by private initiative, a relatively revolutionary development for the late 1920s. From 1930 onwards individuals bought up land in the area and in 1948 the name of Sabi Sand Wildtuin was proposed and the reserve was proclaimed in 1965. The idea of forming a nature reserve in the Timbavati area was mooted in around 1937. The proposal of a game reserve was discussed in 1954 and the Timbavati Private Nature Reserve was proclaimed in 1956 (Porter 1970). A similar pattern is evident for the Klaserie area where by 1936, in addition to cattle ranching, the land was used for hunting (the cost of land at that time was around £1.27 per ha). Cattle farmers were finally bought out in the mid-late 1960s and the Klaserie Private Nature Reserve was proclaimed in 1969.

In the early 1960s the Sabi Sand Wildtuin, Timbavati Private Nature Reserve and Klaserie Private Nature Reserve were separated from the Kruger National Park by the erection of a veterinary fence designed to combat Foot and Mouth disease. The ecological effects of this fence became apparent in 1962 when a drought resulted in the death of large numbers of blue wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*) that were prevented from migrating towards the west.

Cattle farming continued to dominate in the Hoedspruit area to the west of the

Kruger National Park and large private nature reserves until the late-1970s. Then followed a large-scale switch of land-use, with cattle being replaced by game throughout most of the region between the Orpen road and the Olifants and Selati Rivers. The cost of land at this time was approximately R70 per ha. At about this time, the first of the small-scale (200–5000 ha) operations became involved in the ecotourism industry. In 1992, a new era was heralded with the removal of the fence between the Kruger National Park and the large private nature reserves. The latter includes the Sabi Sand Wildtuin and the so-called Association of Private Nature Reserves - Timbavati Private Nature Reserve, Umbabat Private Nature Reserve and Klaserie Private Nature Reserve (Figure 1). At the same time there was ongoing consolidation of properties adjacent to the Associated Private Nature Reserves, resulting in properties ranging in size from 8000 ha to 34 000 ha. The current price of land in the area varies from R3000 per ha to R30 000 per ha.

Bush encroachment – causes and consequences

In the past, herbivores such as blue wildebeest and zebra migrated from the eastern Lowveld west towards the Drakensberg mountains in response to a decline in winter grazing in the western part of what is now the Kruger National Park. In summer, as grazing conditions improved, these animals migrated back again. This resulted in a natural resting of large areas of the Lowveld at certain times of the year. Under these conditions, fire was probably important in maintaining the structure of the savanna ecosystem. The erection of the Kruger Park boundary fence and the sub-division and fencing off of land for commercial cattle ranching, and over the past few decades game ranching, halted these natural migration patterns. Vegetation that was naturally rested for part of the year became heavily grazed by the now sedentary, and often unchecked, herbivore populations on units much reduced in size. Collinson & Goodman (1982) divide herbivores into four types depending on their potential impact on the vegetation. Species such as zebra, elephant (*Loxodonta africana*), white rhino (*Ceratotherium simum*) and buffalo (*Syncerus caffer*) are capable of bringing about drastic changes to climax vegetation (Type I herbivores), which in turn adversely affects poorer competitors

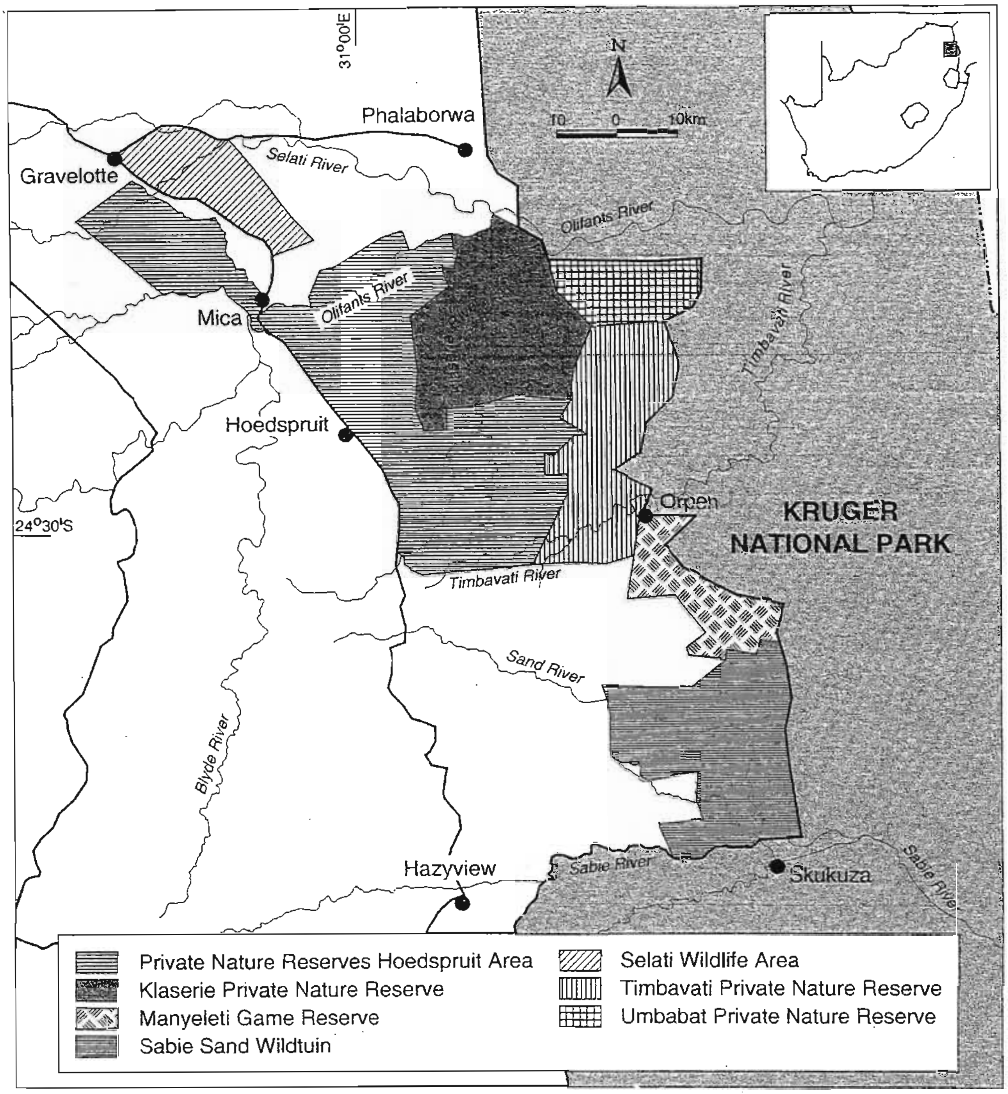


Figure 1 The eastern Lowveld savanna study area (reproduced from publication – University of KwaZulu-Natal Press).

such as sable (*Hippotragus niger*) and roan (*H. equinus*) antelope and tsessebe (*Damaliscus lunatus*) (Type II herbivores) that were previously relatively abundant in the area (White 1951). With fencing it became necessary to provide water artificially year round in areas where water was only seasonally available in the past. As a result the numbers of water-dependent species such as blue wildebeest and impala (*Aepyceros melampus*) increased significantly. These species are able to exploit altered vegetation conditions brought about by the impact of elephant, buffalo and zebra, to the extent that they drive it past the point that would have resulted from use by the latter species alone (Type III herbivores) (Collinson & Goodman 1982). Type IV herbivores are generally browsers and may increase due to changes brought about by Type I and III species, but have little impact on the vegetation (Collinson & Goodman 1982; Peel et al. 1998a).

A similar situation arose in the surrounding communal rangelands where, as early as the 1920s, indigenous communities were allocated less than one sixth of the available land (Stevenson-Hamilton 1929). These areas became densely populated with domestic livestock. Cattle and goat stocking levels were further increased through high survival rates due to a compulsory dipping scheme that largely overcame the many difficulties associated with keeping livestock in the Lowveld region.

The major influence of herbivory involves the interaction of grazing, browsing and fire. Bush encroachment is promoted by heavy grazing (often in conjunction with a reduced browser component) which opens up space where tree seedlings can germinate in the absence of grass competition. This sets up altered tree:grass interactions that include an increase in competition for soil water, often with a resultant increase in woody density – woody species having access to water deeper down in the soil profile due to their extensive root systems (Smit 1992). The major implication of such interactions in the Lowveld savanna is that woody species are, from a game or stock point of view, generally a poor replacement for grasses. A thickening of woody species, particularly in areas where grazers and mixed feeders (e.g., impala) dominate, causes a weakening of the grass layer, resulting in reduced root growth, decreased grass production, exposure of the soil and reduced litter input. This in turn may result in increased exposure to the impact of rainfall, increased soil temperatures, reduced rainfall infiltration, increased run-off, increased soil erosion, lower levels of organic matter in the soil and an increased chance of infiltrating water leaching to soil depths out of reach of grasses. Hot fires, which have the greatest effect on the susceptible woody sapling phase become less frequent due to the weakened grass layer and the woody component is again advantaged (Scholes 1987). Resulting conditions are not optimal for the grazing species which, because of their dominance in the Lowveld savannas, are critical to ecotourism operations. In addition, species such as roan and sable antelope, which are characteristically species of open grasslands and open woodland, also decline. Artificial feeding during drought conditions in some protected areas exacerbates the situation as high animal numbers are maintained on already overgrazed areas.

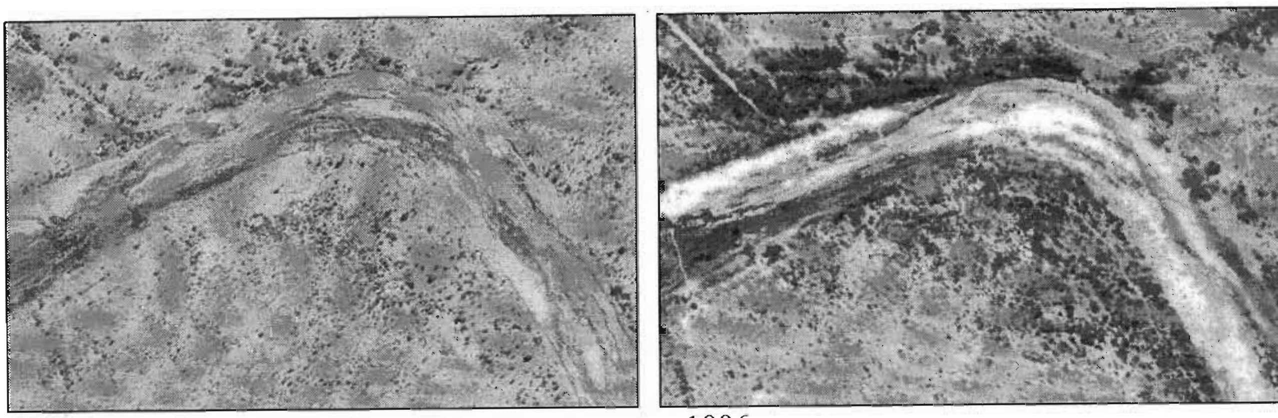
It is important to touch briefly on the complexity of ecological systems.

Hierarchies and adaptive cycles comprise the basis of ecological (and social) systems across scales and together they form what is termed a panarchy (Holling 2001). According to Holling (2001) the panarchy describes how a healthy system invents and experiments and benefits from inventions that create opportunity while avoiding those that may destabilise the system because of their nature or excessive exuberance. Each level (scale) from large through intermediate to small operates at its own pace.

The discussion thus far on the causes of bush encroachment has focused on factors operating at (in ecological terms) small scales (lower levels). Larger scale (higher level) issues relating to possible causes of bush encroachment include the impact of elevated CO_2 levels in the atmosphere on tree:grass interactions. Current levels of CO_2 (360 ppm) exceed values for the last 440 000 years, and the prediction is that by the end of the century these levels may exceed estimated values for the last 5 million years (700 ppm) Bond et al. (2003). Bond et al. (2003) tested the hypothesis that changes in atmospheric CO_2 would change the rates of survival of young trees after burning. They found that trees should disappear from savanna systems where fire is a regular occurrence at low CO_2 levels. This is consistent with paleo-historical records for current South African savanna systems that were previously treeless (Bond et al. 2003). They also simulated the effects of increases in CO_2 from pre-industrial times to the present and found large increases in tree density driven by CO_2 fertilisation of tree growth. The latter suggests that bush encroachment in savanna areas may in part be driven by increasing CO_2 levels in the atmosphere (Bond et al. 2003). The above discussion illustrates that while we may manipulate the tree:grass ratio at relatively small scales (lower levels) we must be cognisant of the fact that there are scales of system functioning over which we have no control. Fine scale interventions may be able to offset these coarse-scale effects to an extent but will now require more effort.

The importance of 'favourable' tree-grass interactions must also be highlighted. These include higher grass production beneath trees due to shade and leaf litter, and fruits and pods which provide nutrients and decrease the splash effect of rain. Highly favoured and productive grasses such as *Panicum maximum* are closely associated with the presence of trees. Furthermore, grass production does not necessarily decline linearly with an increase in woody plant density; the woody component can, under certain circumstances, contribute favourably to grass quality and quantity (Smit 1992).

A comparison of the 1944 and 1986 aerial photographs of the eastern Lowveld exhibit a pattern of increasing woody plant density over extensive areas (Figure 2). Such increases in woody plant density have a negative impact on two of the major land- uses in the area, tourism and the success of rare species such as roan and sable antelope (Carr



1944 1986

Figure 2 Aerial photographs of an area of the eastern Lowveld showing increases in woody plant density from 1944-1986.

1985; Carr 1986a; Carr 1986b; Carr 1988). There is thus a critical need for thinning and coppice control, which is environmentally responsible and cost effective if generating income, and provided appropriate ecological monitoring is in place.

Economic and ecological implications of bush control

Shackleton et al. (1994) showed that the woody standing crop increases with distance from villages in the Mhala and Mapulaneng areas, which are situated adjacent to and to the west and south of the major wildlife areas of the eastern Lowveld. The mean standing crop is 1011 kg/ha close to the villages, 3129 kg/ha in intermediate areas and 13 004 kg/ha in more distant areas. The sustainable harvest of deadwood is 17.2 kg/yr per 1000 kg of live standing biomass (Shackleton 1998). Given the more dense woody vegetation in adjacent protected areas a bush control approach has been taken, i.e. thinning or clearing. It is estimated that 17 000 one-ton truckloads could be removed from 1800 ha in a protected area in 18 months (equivalent to 4092 kg/ha/yr) (Davies undated). A one-third thinning approach based on 13 004 kg/ha would be 4335 kg/ha, while a two-thirds thinning approach would be 8669 kg/ha/yr. In the hypothetical case studies that follow, a farm-gate value for a 650 kg truck-load is taken as R35 (Davies undated), although this may vary considerably.

The use of a professional contractor and trained field staff is recommended as the most efficient approach to control bush (and is therefore included in the calculated costs below). The use of systemic chemicals is favoured as they allow for the selective control of target woody plant species. Costing for bush control is given for two systemic products, Access (active ingredient Picloram) (Reg. No. L 4920) and Tordon-Super (active ingredient Picloram and Triclopyr) (Reg. No. L 3699), that are commonly used in the region (2001/02 costing). It must be remembered that bush control is seldom a once-off operation and follow-up treatment is usually necessary. The success of clearing operations is gauged by the length of time that the area remains open, while maintaining a good herbaceous species composition, cover and production. Sites should be re-visited to determine the amount of coppice, suckering and natural recruitment of tree seedlings in order to determine the type and timing of further treatment. In considering the ecological aspects of bush control (below) we report only studies that provide ecological data both before and after the bush control programme.

The costs for a thinning approach using correctly a 2% mixture of Access together with Actipron (an emulsifiable oil for use as an adjuvant) and water with a dye added is in the region of R1200 per ha (R1000 per ha for sparse woodland and R1400 per ha for thicker woodland). The cost of re-treatment and follow-up is approximately a quarter that of the initial treatment (R300–R500 per ha). Foliar application, using a 0.75% mixture of ingredients as described above, is commonly used as a re-treatment method where re-sprouting does not warrant the more costly mechanical approach. The costs of a thinning approach using a 1% mixture of the chemical Tordon-Super mixed with diesel and a dye added is approximately R1600 per ha (R1200 per ha for sparse woodland and R2500 per ha for thicker woodland). The cost of re-treatment and follow-up varies between R600–R1500 per ha. Both of the above operations are carried out as cut stump treatments (10–15cm above the ground) and costs include labour, equipment and chemicals.

Both Access and Tordon-Super are considered effective in killing trees if correctly applied. Access is cheaper largely because it is applied with water as a mixer as opposed to Tordon-Super which is mixed with diesel. A further advantage of the water based, as opposed to the diesel based, product is that the dead stumps break down more quickly.

Because of their extensive root systems, species such as *Colophospermum mopane* and *Pterocarpus rotundifolius* trees are not always killed by the first treatment. These species tend to sucker from the rootstock, and often require a follow up treatment when they begin to impede game viewing. The current return time for re-treating *Colophospermum mopane* in the eastern Lowveld is three to three and a half years, which is considered highly satisfactory (Peel 2002a; Peel 2002b).

Management scenarios affecting the value of wildlife operations

Valuing wildlife at market price reflects what people are willing to buy and sell goods for. Wildlife incurs management and infrastructure costs as well as costs of wildlife impact on other resources (such as infrastructure and crops) and opportunity costs. If wildlife conservation can generate net positive revenues then this is a major incentive to conserve it. In the case studies below we therefore examine land and game prices (live capture and hunting), lodge rates/costs, and wood use values/costs (figures are given in Table 1). Six hypothetical management scenarios are presented for six lodges and wildlife enterprises. These are based on actual case studies and include the economic and ecological implications of bush control.

1. Ecotourism – Greater Kruger National Park (South)

The primary objective of this lodge is ecotourism within an inherently highly productive savanna ecosystem. The lodge falls within a reserve that is a preferred destination for the international market and offers luxury accommodation and the Big Five (elephant, rhino, buffalo, lion and leopard) as a major attraction.

Table 1. Baseline information (income and expenditure – 2001/02 figures) entered into the models for the different management scenarios (case studies 1–6) examined in terms of the economic implications of bush control programmed in the eastern Lowveld of South Africa.

	Case study					
	1	2	3	4	5	6
Size	2000 ha	2000 ha	3500 ha	2700 ha	2000 ha	29 500 ha
No. beds	30	30	20			7[1]
Occupancy rate	40%	40%	40%			20%[1]
Expenditure						
Land price (per ha)	R20 000	R12 000	R4000	R4000	R3250	R4000
Land levies (per ha per yr)	R485				R240	
Cost to lodge (ppn.[2])	R730	R700	R327			R247
Reserve running costs (per ha per yr)			R50	R185		R35
Income						
Lodge rack rate (ppn.[2])	R2400	R2100	R980			R740
Sustainable game removal[3]			R56	R482	R39	R99
Landowner levies (per ha per yr)					R240	

[1] Hunters; [2] Per person per night; [3] Farm gate value

2. *Ecotourism – Greater Kruger National Park (North)*

The primary objective of this lodge is ecotourism in an arid, less productive environment than case study 1. The lodge is in an internationally renowned area, although less so than case study 1, and offers luxury accommodation and the Big Five as a major attraction. The reserve was previously cleared in an *ad hoc* fashion resulting in thick stands of coppicing *Colophospermum mopane* veld. This was not aesthetically pleasing and negatively impacted on game viewing. The overall management objective is to conserve a wide diversity of large herbivores as a base for outdoor recreation and to optimise revenue through the wise use of natural resources in the area.

3. Ecotourism – small fenced property (Central)

The primary objective of this lodge is ecotourism in an arid environment. Again, the lodge offers luxury accommodation and the Big Five as a major attraction. However, unlike case studies 1 and 2, this lodge operates within a fenced area of 3500 ha and targets a different client-base with lower rack rates (rates charged per person per night). In addition to the income derived from tourism, a fenced property such as this can diversify its operations. Because of the size of the property and the need to show visitors high numbers of animals and a diversity of species there is a danger of overstocking, with negative consequences such as bush encroachment. Such operations can utilise excess game through live removal. Data collected since 1990 indicate that a wide spectrum of game can be sustainably removed on an annual basis (Peel 2002a; Peel 2002b).

4. Rare species breeding – small fenced property (West)

The primary objective of this operation is the breeding of rare and endangered species on 2700 ha in a high rainfall area. When the property was purchased it was heavily encroached with *Dichrostachys cinerea* at up to 15 000 stems per ha, greatly lowering its production potential. A large-scale bush control programme was launched at considerable cost and the property was extensively thinned to return the habitat to one which was favourable for the production of roan and sable antelope. The management objective was to maximise the production of these antelope species and to optimise revenue through their wise use. In order to minimise competition with other herbivore species, a live game removal programme and some hunting is possible.

5. Recreation – small fenced property (North)

This property is game fenced and covers an area of 2000 ha under a share-block scheme. It has largely been purchased with discretionary income. Income generation is not important and share-block members use the land for recreational purposes. The property does however generate income through sustainable live game removal (Peel 2002a; Peel

2002b).

6. Recreation – Large fenced property (North)

This property is game fenced and covers an area of approximately 30 000 ha under multiple land ownership. The size of the property lends itself to the sustainable use of herbivore species through live capture and hunting and available data indicate that these two land-uses are sustainable. The breeding of sable in the area is still to be optimised and this has the potential of bringing in significant income in the longer term. The hunting of Big Five species when the opportunity arises also has excellent potential.

Methods

Economic aspects of bush control

To examine the economic aspects of bush control the following approach was adopted (figures were based on 2001/02 figures. An annual increase in costs of between 10 and 12% is considered realistic). For each of the six case studies, five scenarios were examined:

1. Cost of initial thinning using Access at R1000 per ha per yr (moderately thick bush);
2. Cost of initial thinning using Access at R1400 per ha per yr (thick bush);
3. Cost of initial thinning using Tordon-Super at R1600 per ha per yr (moderately thick bush);
4. Cost of initial thinning using Tordon-Super at R2200 per ha per yr (thick bush); and
5. No bush control.

Models were based on an initial treatment followed by re-treatment in year n+3, n+6 and n+9. Year 1 costs are calculated for 25% of the land area of the property except for case study 6 where, due to the large size of the property and the concomitant practical constraints attached to treating large areas effectively, a figure of 10% was used. Year n+3, n+6 and n+9 costs are calculated at 33% of the effort compared to year 1. Finally, thick bush was estimated to return at approximately 8669 kg/ha/yr and moderately thick bush at approximately 4335 kg/ha/yr (based on Shackleton 1998).

Actual figures from the reserves relating to income, costs and other factors (Table 1) were entered into the models (2001/02 data). From these a net figure was estimated for each year over a 10-year period. The cost of any capital was included as a cost at the beginning of the period and this was added again (as income) at the end of the period. On this cash stream the Internal Rate of Return (IRR) was calculated. The IRR essentially provides an indication of the percent return to an investor on their capital over a fixed period, including the timing and magnitude of cash inflows and outflows. However, the following factors must be borne in mind when interpreting the results of the IRR.

First, the value of the land, which includes game and infrastructure such as buildings, roads, fences, is assumed to be the same at year 1 as at year 10. This assumes therefore that the assets are maintained in good working order over the life of the project, the value of the land and the game do not change over that period and inflation is set at zero. In reality this is unlikely as land value has increased at around 25% per annum over the last 25 years (J. Joubert pers. comm. – Johan Joubert Properties Hoedspruit). The price of game has also increased, at least in real terms. However, it is assumed that such increases would apply for all the properties considered and therefore that any error is evenly applied to all the management scenarios examined.

Second, it was not possible in most instances to determine what would have occurred if bush thinning had not taken place as no control studies were undertaken. Income generated in almost all situations would probably have decreased as game viewing (tourism potential) or production would have been reduced. The comparison between thinning and not thinning is merely to indicate the costs of clearing rather than the option to not thin. Case study 4 would simply not have been able to breed rare game if it had not been thinned. However, what the model does show is that clearing is a small percentage of the costs when compared with the cost of land, infrastructure and game.

Ecological aspects of bush control

We examined the ecological impacts to date of bush thinning programmes in the eastern Lowveld in relation to the stated objectives of the land user in the described areas using 200 m^2 belt-transects. The nearest plant method was used to measure herbaceous species composition and cover (based on tuft size and distance to plant) together with the composition, density, canopy cover, and structure of the woody layer (Peel 1998b). In the herbaceous layer, both annual and perennial species were recorded accounting for bias expected from varying environmental conditions. Only those case studies with ecological data from before and after the bush control programme were included; namely case studies 2 and 4, above.

2. Ecotourism – Greater Kruger National Park (North)

A monitoring study was initiated to assess the ecological impact of a bush removal programme at the local scale, and its long-term sustainability. Vegetation change was determined in terms of trends in (1) woody species composition, (2) herbaceous species composition and cover, (3) woody plant density, and (4) grass production. Studies were set up within three pairs of adjacent sites. Within each pair of sites, one was cleared and the other was not. The sites were permanently marked on the ground using concrete blocks, and accurate instructions for their relocation were made. Vegetation monitoring has been carried out on an annual basis since 1995.

4. Rare species breeding – small fenced property (West)

Again, a monitoring study was initiated to assess the ecological impact of a bush removal programme at a local scale, and its long-term sustainability. This includes determining vegetation change in terms of trends in herbaceous composition and production. Because Type II herbivores (see earlier discussion), such as roan and sable antelope, need lightly utilised veld, the long-term management of this property aims to increase the proportion of Increaser I and Decreaser species. Increaser I species are herbaceous species that increase when the veld is moderately underutilised and Decreaser species are herbaceous species that predominate in good condition veld but decline when veld is overutilised (and in instances when the veld is extremely underutilised) (Hardy et al. 1999). Trends in herbaceous canopy cover are monitored, with the goal of maintaining the level above 25% to minimise raindrop impact and maximise rainfall infiltration (Venter 1988). The structure of the herbaceous component is also important as roan and sable antelope appear to be sensitive to close cropped veld, with roan grazing down to a height of 8 cm and sable to 6 cm (Carr 1988). Reduced grass height forces these species to move out of a particular area. Woody plant density is also monitored. Study sites were set up across the reserve in three different rainfall areas to determine whether or not the objectives of the bush thinning programme are being met. There are no control sites on this property. The sites were permanently marked on the ground and accurate instructions for their relocation were made. Vegetation monitoring has been carried out on an annual basis since 1991.

Results

Economic aspects of bush control

1. Ecotourism – Greater Kruger National Park (South)

The IRR over ten years indicates that case study 1 is financially viable (Figure 3). The profitability of this operation is good. However, although the rack rates achieved under this management scenario are higher than in case studies 2 and 3 the IRR is lower because of the initial high price paid for the land and, to a lesser extent, the land levies imposed on this property.

2. Ecotourism – Greater Kruger National Park (North)

Despite lower rack rates compared to case study 1, this property shows a higher IRR over ten years (Figure 3), primarily as a result of the lower land prices in this area and the fact that no land levies are paid.

3. Ecotourism – small fenced property (Central)

The IRR of this management scenario is only marginally less than that of case study 2 over ten years (Figure 3). The lodge is in a positive financial position in the medium-term. Although the rack rates charged are less than half those of case studies 1 and 2 the price of land is markedly lower than areas within the 'Greater Kruger National Park'. Because of the need for intensive management on these smaller fenced properties, additional income can be via game removal programmes and hunting.

4. Rare species breeding – small fenced property (West)

Through careful planning and judicious management (e.g. increasing the production of roan and sable antelope through the intensification of the breeding programme) this scenario is economically viable over ten years (Figure 3). The calculations assume that a viable population of rare and endangered species is present on the property. As with the previous case study, the need for intensive management on these smaller fenced properties allows for diversification of activities through game removal or hunting of surplus animals that compete with the focus species. It is important not to make sweeping statements about the 'lower' profit margins on this property because there is no control property to compare it with. It can safely be assumed that without the bush control programme the productivity of the land would be lowered with a concomitant lowering of the profitability of the operation.

5. Recreation – small fenced property (North)

This management scenario is marginally financially viable but only if no bush control programme is implemented (Figure 3). The potential to increase the cost of buying into such schemes will be increased through better game viewing possibilities. Because of the lower profitability of this property compared to the previous cases, management must be geared towards maximum sustained yield of game species for live removal. The consolidation of small properties into larger units would improve the economic margins and at least cover the costs of a bush control programme.

6. Recreation – Large fenced property (North)

Because of the size of this property, returns on wildlife utilisation are currently low (Figure 3). The profit margins are lower than in case studies 1–3 and management should be geared towards maximum sustained yield of game species for live removal (in particular captive breeding), as well as hunting.

Ecological aspects of bush control

2. Ecotourism – Greater Kruger National Park (North)

The sites which have undergone bush clearance have a consistently higher proportion of perennial grasses than the sites which were not thinned (Figure 4a). Note the lag of one season between rainfall and perennial grass response. For example, the high rainfall of the 1995/96 season effectively buffered the below average rainfall 1996/97 season and the very dry 1997/98 season. This is particularly apparent on the thinned sites with their higher proportion of perennial grasses. The very high rainfall of the 1989/99 and 1999/00 seasons will most likely maintain the current high proportion of perennial grasses in the short-term.

Basal cover (distance and tuft measures) is markedly higher on thinned vs. unthinned sites (Figures 4b and 4c). Again there is a time lag of one season in the response of the cover variables to rainfall.

Primary production is a measure of the amount of material produced by the herb layer in a season, and it determines how much forage and fuel there is available in a particular area. Herbaceous production is consistently and markedly higher on the thinned versus the un-thinned sites (Figure 4d). The relationship between herbaceous production in a year and the rainfall for the same year is illustrated (e.g., 1997/98 drought and resulting low grass production, and the very high rainfall 1999/00 season and resulting high grass production).

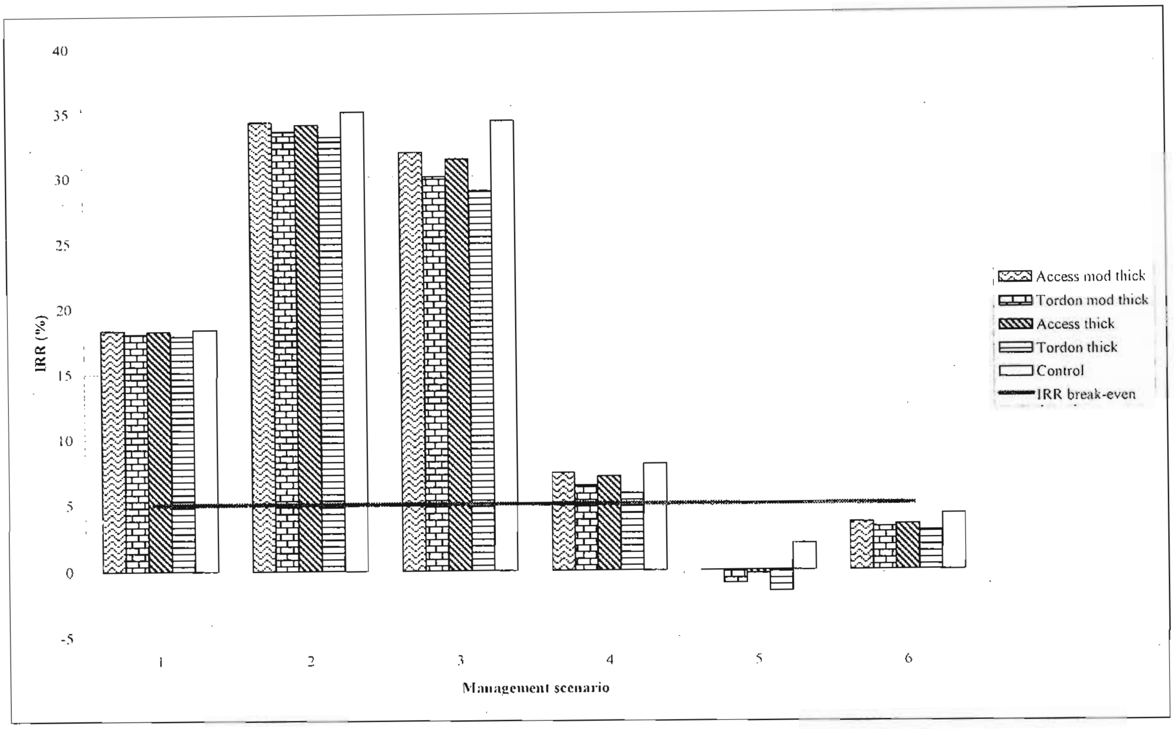


Figure 3 Internal rates of return (IRR) for six properties with different management scenarios (see text) under four different bush thinning strategies versus no bush thinning (control).

Areas that had undergone bush thinning thus maintained a relatively high percentage of perennial grasses, a favourable grass cover (basal cover index and tuft diameter) and higher grass production levels than areas that were not thinned. The thinned areas also had an improved visibility and game viewing potential, important in terms of the management goals of this property, and contributed to biodiversity in that they offer an open habitat within relatively closed surrounding *Colophospermum mopane* woodland.

4. Rare species breeding – small fenced property (West)

Increaser I species showed an encouraging increase during 1999/00 to their highest levels since the beginning of the project, while relatively high proportions of Decreaser species are also being maintained (Figure 5).

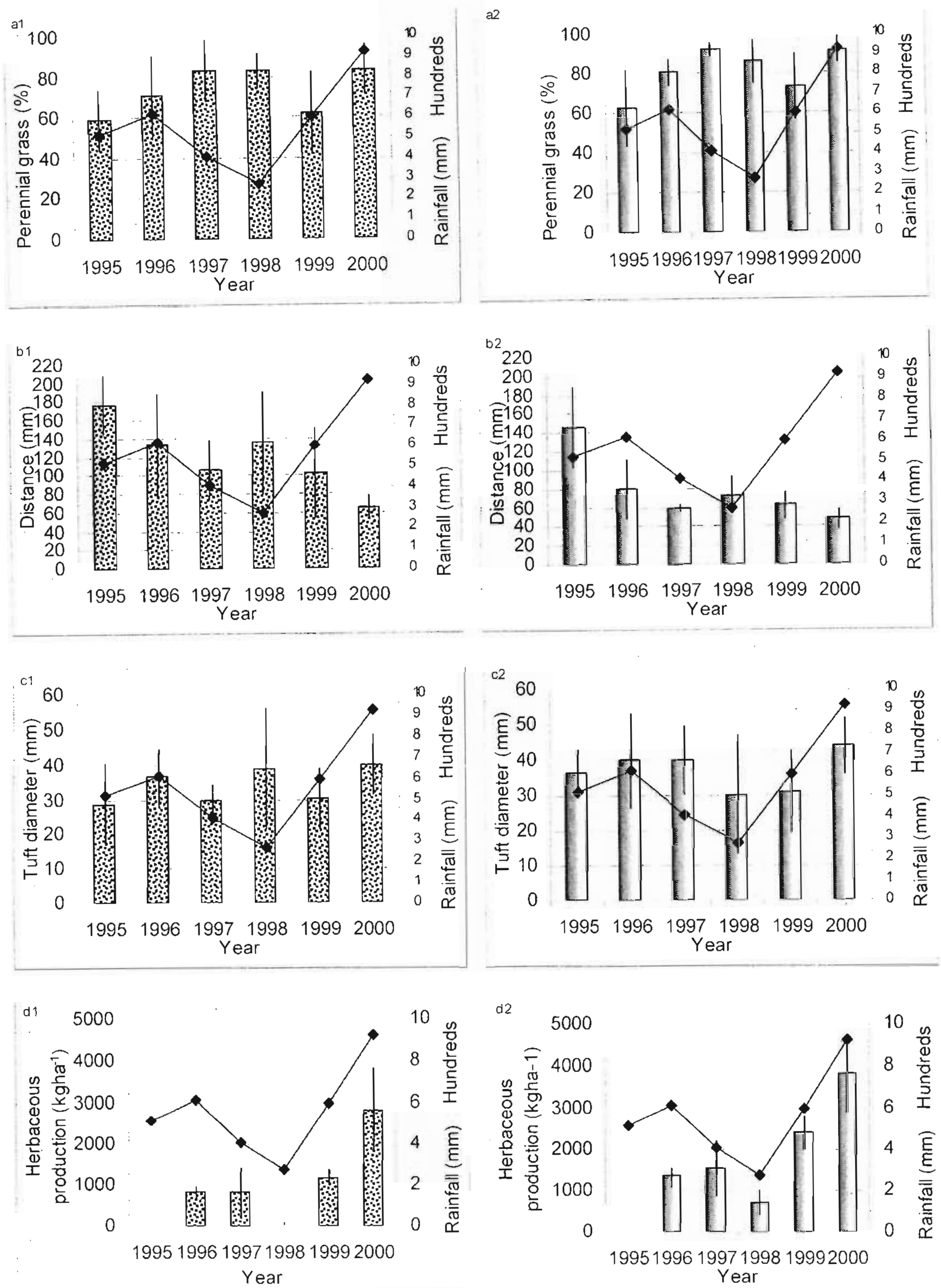


Figure 4 Case study 2 – a comparison of sites that have not been cleared (prefix followed by 1) of bush (thinned) versus sites that have been cleared (prefix followed by 2) in terms of (a) proportion of perennial grass, (b) herbaceous perennial cover (distance), (c) herbaceous perennial cover (tuft diameter), and (d) herbaceous production. Bars indicate standard deviation.

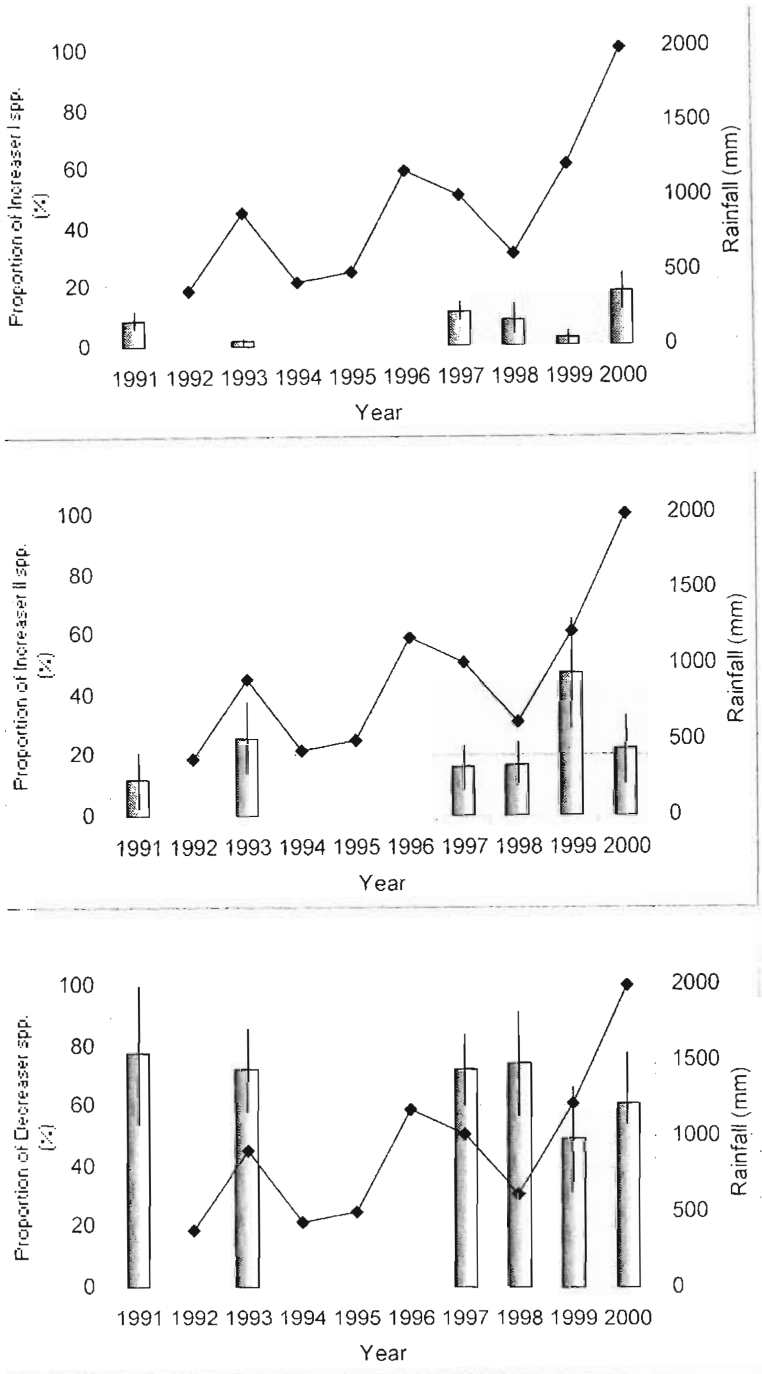
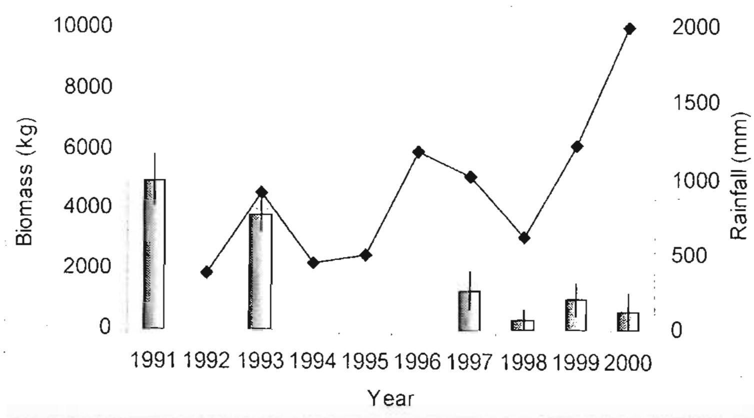


Figure 5 Case study 4 – proportion of Increaser I (top), Increaser II (middle) and Decreaser (bottom) species following a programme of bush control. Bars indicate standard deviation.

Figures 6 and 7 show the total biomass available and percentage of the total biomass available for roan and sable antelope. Both parameters are important as they are not necessarily correlated. Thus, although there may be more total forage available under a programme of bush clearance, there may be proportionally less available for the species of particular interest. Although driven largely by rainfall, declining levels of production and/or percentage available for roan and sable antelope may also indicate high levels of feeding competition from species such as zebra or blue wildebeest or management intervention.



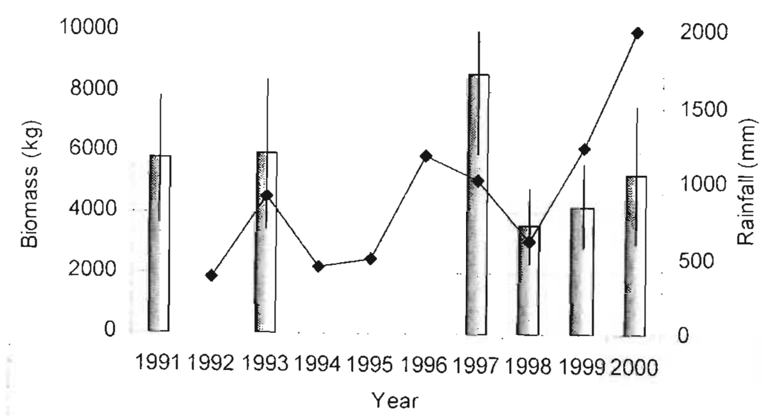


Figure 6 Case study 4 – total herbaceous plant biomass available for utilisation by roan antelope (top) and sable antelope (bottom) following a programme of bush control. Bars indicate standard deviation.

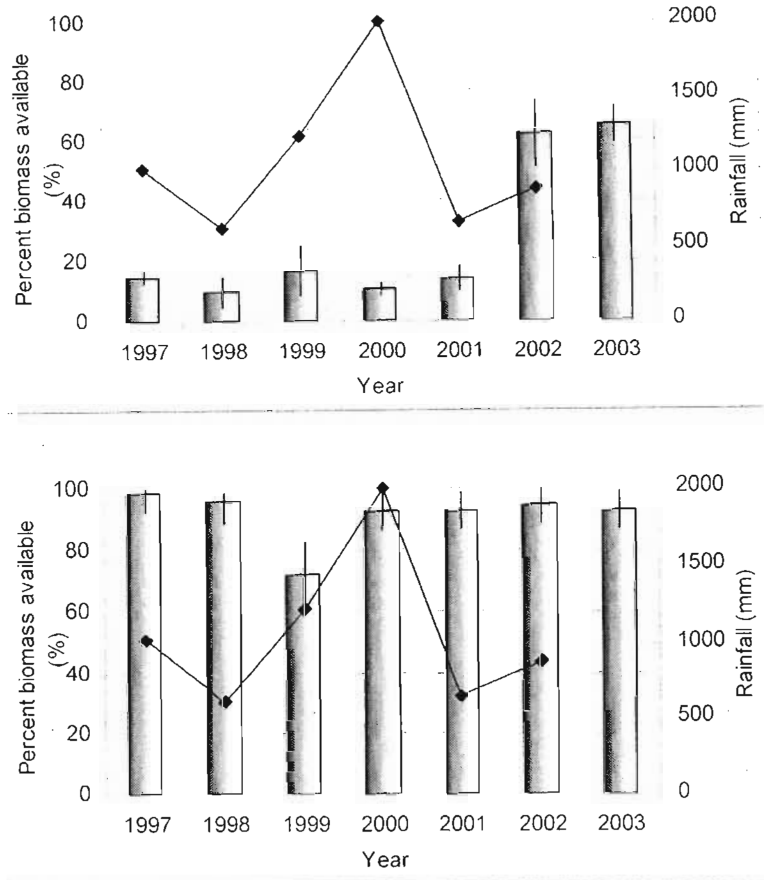


Figure 7 Case study 4 – proportion of herbaceous plant biomass available to roan antelope (top) and sable antelope (bottom). Bars indicate standard deviation.

The mean herbaceous canopy cover was above the critical limit of 25% to maximise rainfall infiltration (Figure 8). Mean grass height declined despite a high rainfall season but was above the critical limits for roan (8 cm) and sable (6 cm) (Figure 8).

The value of vegetation monitoring following the bush thinning programme is illustrated by the observation that those parameters critical for the successful breeding of roan and sable antelope are being maintained. Management can be (and is) largely directed at species such as zebra, blue wildebeest and impala that compete directly with roan and sable antelope (Collinson & Goodman 1982). Intrinsic rates of increase of 20–30% for the rare species in question indicate that the habitat manipulation programme has been successful in this extensive system. Ongoing herbivore management and an

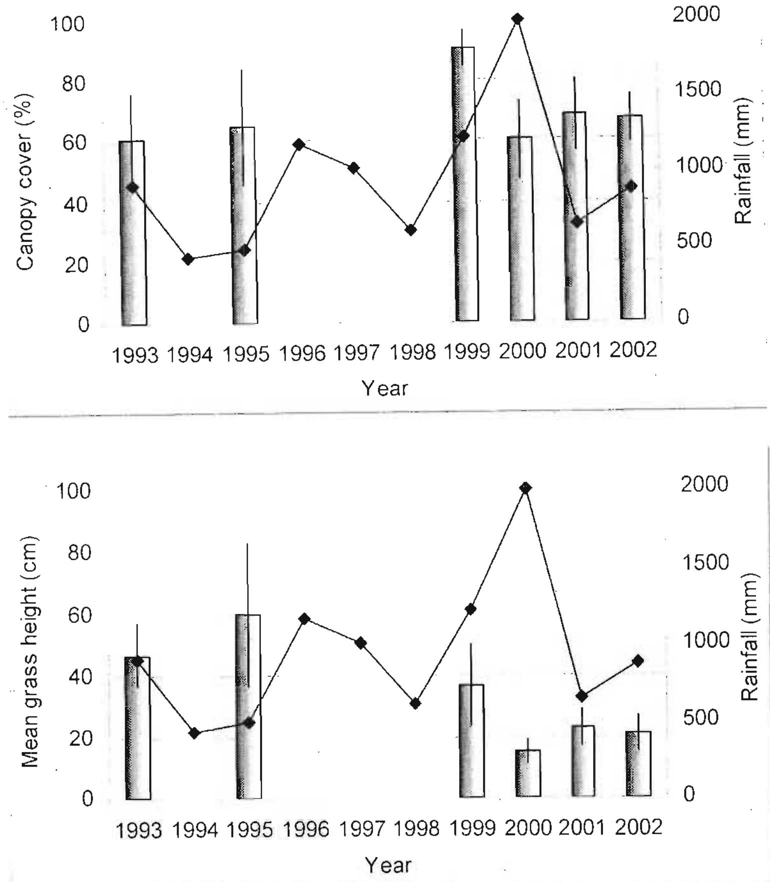


Figure 8 Case study 4 – the proportion of herbaceous canopy cover (%) (top) and mean grass height (cm) (bottom) following a programme of bush control. Bars indicate standard deviation.

adaptive management approach to burning are critical in the success of this breeding programme.

Discussion

It is encouraging to note that all six management scenarios examined yield positive financial returns after a ten-year projection of the modelled parameters. In addition, five of the six operations showed a profit, albeit at reduced margins, when bush control was implemented. It is obvious that the cost of bush control increases with increasing bush density and a thinning approach is advocated particularly in less dense areas. Besides reducing the costs associated with the greater effort required, this would improve game visibility and ultimately the viewing experience (which is difficult to quantify). The latter may in turn have a positive spin-off on occupancy rates in the lodges. Further, the grazing resource is generally limiting and a reduction in the tree:grass competition would benefit grazing animals while improving the chances of prey species in detecting predators (this would also be true in case study 4 – the breeding of rare species).

The wide range of land uses makes direct comparisons difficult. However some conclusion can be drawn from the operations. In areas where land is more expensive, the game viewing and therefore structure of the bush is important (thinning is likely to be a greater factor). It is critical that a good game-viewing product is offered to justify the high rate charged to guests. The lower IRR on such a property compared to others is significantly influenced by the high price of land. Consequently if the occupancy rates charged to guests should fall these owners are more vulnerable to suffer higher losses than those on less expensive properties. Obviously, investors invest for reasons other than those presented here. Ecotourism has the ability to increase the profitability of an area and as it is usually not tied to the productive capacity of the veld it can add value beyond this. Diversification of activities through the removal of surplus game (particularly on fenced properties) increases the chances of an operation being economically and ecologically viable.

While initial costs of bush control programmes are high, the objective is to decrease the return time and therefore costs for re-treatment. The return time on programmes examined here is between three and three and a half years, which is highly satisfactory and increases the economic viability of conservation enterprises due to improved ecological conditions.

Data presented suggest that bush control (thinning) programmes, if properly planned and implemented, can be ecologically sustainable and may increase the value of land through, for example, improved game viewing for ecotourism and increased grass production. However, ongoing monitoring and management is critical in maintaining environmental conditions that will achieve the objectives of the land user.

Acknowledgements

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Chapter 3

A phytosociological description of private nature reserves adjoining the west of the Kruger National Park using remotely sensed and ground-truthed woody data

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Abstract

We provide a description of vegetation patterns of the areas under conservation management to the west of the KNP at a spatial scale that allows for the meaningful examination and comparison of the structure, functioning, and ultimately effective management, of these savannas. A Two-Way Indicator Species Analysis (TWINSPAN) based on composition and structure was applied to the relatively stable woody component. The resulting TWINSPAN classes for individual monitoring sites were used in two separate supervised classifications of Landsat ETM^+ imagery across the study area. The co-ordinates of the training sample (data used to develop models) were fed into a GIS and the resulting TWINSPAN point-feature shapefile processed using an Inverse Distance Weighted (IDW) interpolation and 1 km theme-buffer function. The supervised classification using the theme-buffer signatures yielded a satisfactory overall accuracy (Kappa = 0.56; r^2 = 0.66; p=0.05) using a test sample (data used for sensitivity analysis) compiled by reserve wardens throughout the study area. The derived vegetation map was smoothed using a majority filter and after on-screen digitizing a small gabbro intrusion, it was accepted as the best representation of the woody vegetation of the study area at a scale of 1:250 000. Seven plant communities were identified in the current study and satisfactorily accommodated within various topographical units of four extrapolated Landscapes of the Kruger National Park. This contribution thus links to the co-ordinated effort extending into the Trans-Frontier National Park in Mocambique. A key objective of this study is to better understand the functioning of these savanna systems for effective management and we discuss some of the key ecological issues within the plant communities of each Landscape. The latter illustrate the usefulness of the technique in practice.

Key-words: Savanna; pattern; scale; management; Trans-frontier Conservation Areas

Introduction

Up until the 1990's research work relating to wildlife in the eastern Lowveld was focused almost exclusively on the Kruger National Park (KNP) and dealt largely with the preservation (total protection) of particular species of wildlife as opposed to conservation (wise utilization of natural resources). Work at the landscape scale was mostly descriptive and vegetation inventories, at various resolutions, exist for the KNP, Manyeleti Game Reserve and some of the Adjacent Private Protected Areas (APPA) but with little translation of the information into their effective management (Bredenkamp 1982; Zambatis 1982; Coetzee 1983; Gertenbach 1983; Venter 1990, van Rooyen *et al.* 2005).

The broad programme of which this investigation forms a part examines savanna vegetation dynamics across a range of land-use objectives and spatial scales. The degree of management required depends on the scale of interest, for example, the KNP (*c.* 20,000 km^2) has adopted the Noss (1990), definition of biodiversity as an underlying philosophy of their revised management plan (Braack 1997a; Braack 1997b). This approach may even include the desirability of having a certain limited percentage of land in a 'degraded' condition for a period of time to provide habitat ranges to aid biodiversity (Peel *et al.* 1998). Anthropogenic re-scaling, where man rescales patterns in time and space (Urban *et al.* 1987), has been exacerbated through, for example, the erection of fences and the provision of artificial drinking water for game. This is highlighted in the 'intermediate' sized private nature reserves (varying from 200 km^2 to 900 km^2) adjacent to the KNP which, while embracing the basic philosophies of the KNP management approach, and even having similar general objectives, function on different spatial scales (Peel *et al.* 1998). Similarly, fenced reserves (up to 200 km^2) to the west of the larger intermediate scale reserves, where little or no movement is possible, may have similar objectives but, due to their size, present a unique set of management challenges (Peel *et al.* 1998) and often fail to meet the objectives set for them. The APPAs comprise smaller land units and there is a tendency to rehabilitate degraded areas because, relative to the size of the property, they give the impression of a poorly managed landscape. These fenced areas, managed in isolation (man-dominated), provide empirical observations from which to deduce critical thresholds of interaction among components and give insights into the effects of ecological scaling (Peel *et al.* 1998). Management at local scales has, in turn, a potentially critical impact at both regional and global scales, the direct effect of changing the degree of interaction among patches altering system behaviour and ultimately influencing higher level processes (Urban *et al.* 1987).

To meaningfully compare areas of similar ecological potential under different management regimes, there is a need for ready access to generic, low-input, high-return classification and survey methods (Gillison 2002). This level of urgency demands a break from traditional, logistically demanding methods that focus on highly detailed inventories of restricted areas with limited potential for extrapolation. Instead, the emphasis should be on methods that can provide a rapid overview of environmental variability and the manner in which the vegetation responds to change along environmental and management gradients at a landscape (expressed at say 1:250 000) scale. A landscape in this context is defined as 'an area with a specific geomorphology, climate, soil vegetation pattern and associated fauna' (Gertenbach 1983). Landscapes function at spatial and temporal scales that correspond with those of large ecosystems, biomes or communities (Allen *et al.* 2003). So large landscapes link easily with the processes of both smaller and larger ecosystems thus giving us an insight into ecosystems, biomes and community processes (Allen *et al.* 2003).

The classification section portrays recurring patterns of the dominant woody vegetation types, and using soil and landform characteristics (Gertenbach 1983; Venter 1990) a description is presented of plant communities within landscape types in protected areas to the west of the KNP. The latter conforms to the classification of Gertenbach (1983) and Stalmans (*et al.* 2004) whose studies covered the KNP and a part of Mocambique that falls in the newly formed Trans-Frontier Park. This contribution takes the descriptive phase a step further by examining some key environmental and management issues within identified plant communities of the various landscapes. The results allow for the examination and comparison of environmentally similar sites that will contribute to a better understanding of the structure and functioning of these savannas as well as ultimately facilitating their effective management.

The study area

The study area (*c.* 5 000 km^2) is located in the eastern Lowveld of South Africa to the east of the Drakensberg escarpment, between 30°35'E and 30°40'E and 24°00'S and 25°00'S (Fig. 1). The mean annual rainfall varies from around 400 mm in the north of the study area to around 650 mm in the south.

Geologically, the study area is dominated by ancient granitoid rocks of Swazian and Randian age, which are grouped together as Basement complex. The majority of rocks in the Basement complex can be classified as gneiss, granite or migmatite (Venter 1990). The Timbavati Gabbro (consisting of Intrusive Rocks) intrudes into the Basement complex and is exposed at the surface as irregular and discontinuous sills and dykes (Venter 1990). The Gabbro consists of medium to coarse-grained olivine, clinopyroxene, plagioclase, and minor biotite and magnetite.

The study area is situated entirely in the Savanna Biome. Acocks (1988) divides the study area into Lowveld, Arid Lowveld and Mopani Veld, while Low & Rebelo (1996) classify the area into Mopani Bushveld, Mixed Lowveld Bushveld, Sweet Lowveld Bushveld, and Sour Lowveld Bushveld.

Materials and Methods

As stated, a meaningful classification of the vegetation at an appropriate scale is required to facilitate a comparison of key ecological indicators between environmentally similar but discrete units with different management regimes.

Remote sensing techniques have been widely used in South Africa as a tool for mapping vegetation (van den Berg 1993; Fortescue 1997; Lewis. 1998). These techniques make use of electromagnetic energy, which is either emitted or reflected by objects, to study and monitor natural and man-made processes that take place on the Earth's surface (Campbell 1996). However, the analysis, classification and (visual) interpretation of

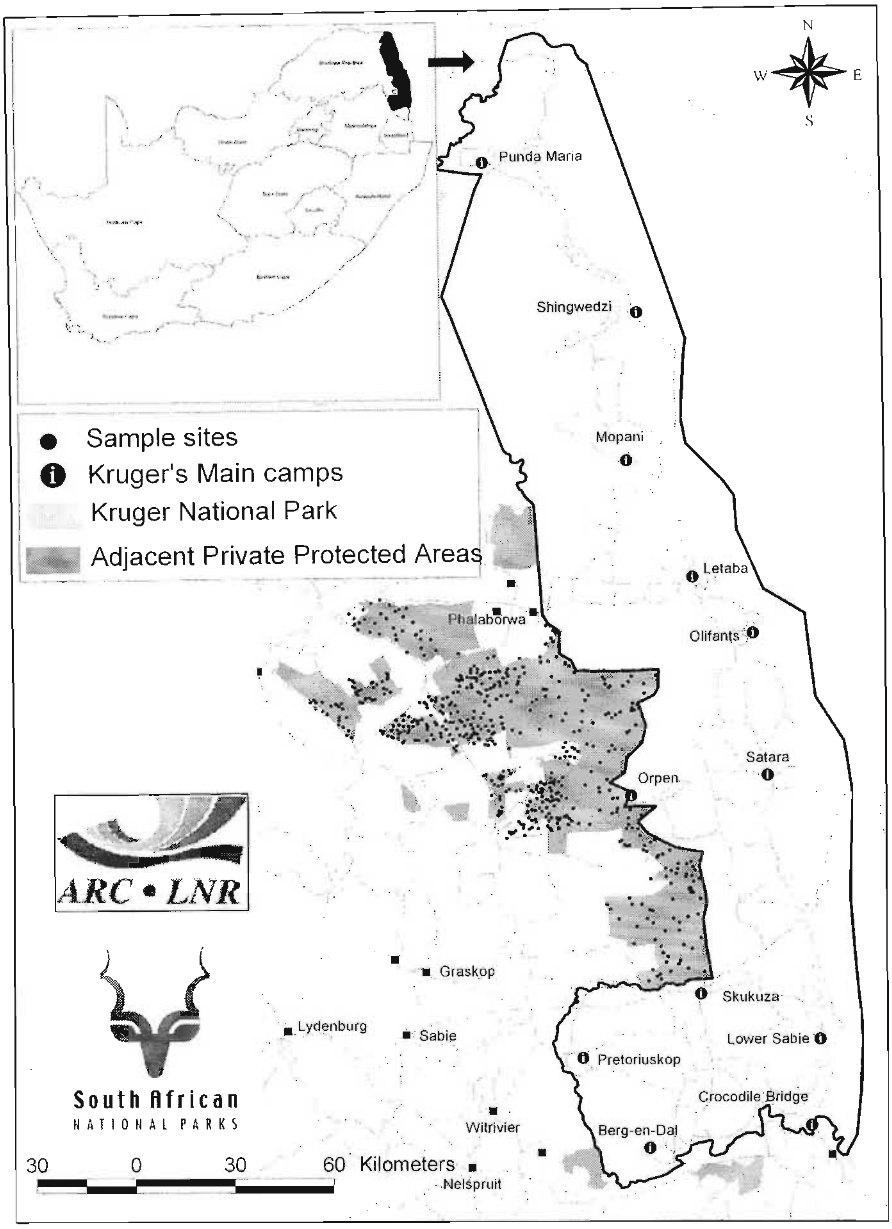


Figure 1 Location of the study area.

remotely sensed data requires prior knowledge of underlying physical, biological and chemical processes that contribute to certain reflectance or emission spectra.

Two Landsat ETM$^+$ scenes (path 168 row 077 and path 169 row 077) recorded 28 April 2001 and 21 May 2001 respectively, were used in this analysis. Both images were radiometrically and geometrically corrected according to U.S Geological Survey (USGS) standards (L1G). ETM$^+$ bands 1 – 5 and 7 were used in a maximum likelihood algorithm for supervised classification with ground-truthed training data. The training sample was obtained from the ARC vegetation-monitoring programme, which consists of 610 annually monitored sites. At each site, herbaceous composition and cover and woody composition, density, canopy cover and physiognomy is determined within a 200 m^2 belt. The dynamic nature of the herbaceous layer is such that the classification was based on the more stable woody component. A Two-Way Indicator Species Analysis (TWINSPAN) was therefore applied to this temporally and spatially relatively stable woody component (Hill 1979).

The woody data

Woody data were numerically classified using TWINSPAN (Hill 1979) based on density values (Singh, Reddy & Singh 1995). The description of the various plant communities obtained from the TWINSPAN are presented hierarchically as follows:

1. indicator species: based on the premise that a group of samples that constitute a community type will have a corresponding group of species that characterize that type. Indicator species ordinate near either end of the ordination axis;
2. dominance is linked to this and is a reflection of fidelity to the group as well as abundance (as defined by pseudospecies cut levels); and
3. preferential species: are species that are at least twice as likely to occur on the negative side of the dichotomy as on the positive side and visa versa. Non-preferential species are those species that achieve at least a 20% frequency on either side.

Once a plant had been described in the hierarchy, it is not repeated in subsequent levels. Large-scale ecological survey work aims at identifying broad patterns in vegetation and the resulting plant communities are summarised in a single synoptic table.

Vegetation physiognomy was incorporated in the classification to delineate communities based on four physiognomic classes (0-1 m, 1.1-2 m, 2.1-5 m and >5 m). Physiognomic data were further analyzed using the classification developed by Edwards (1983) as follows:

1. a primary set of growth forms viz. woody trees and shrubs and non-woody grasses and herbs;
2. a set of projected crown cover classes expressed as a percentage (vertical projection of the crown or shoot area of the plant onto the ground) and the mean number of crown diameters by which plant crowns are separated. The resultant primary cover classes given as % cover and crown:gap respectively are: scattered (<0.1 %; >30), sparse (0.1 – 1 %, 8.5 – 30), open (1 – 10 %, 2 - 8.5) and closed (10 – 100 %, 0 - 2);
3. a set of four height classes for trees, shrubs and grasses/herbs respectively viz. Low (2 – 5 m, < 0.5 m, < 0.5 m), short (5 – 10 m, 0.5 – 1 m, 0.5 – 1 m) , tall (10 – 20 m, 1 – 2 m, 1 – 2 m) and high (<20 m, 2 – 5 m, >2 m); and
4. shrub substratum used to define thicket and bushland.

Integration of remotely sensed and ground-truthed data

The resulting TWINSPAN classes for the training sites were joined to a GIS point-feature shapefile and processed using an Inverse Distance Weighted (IDW) interpolation and 1 km theme-buffer function to create target areas for image interpretation:

1. IDW Interpolation: Sites were used in an interpolation to create a predictive TWINSPAN vegetation surface. A majority filter was applied to the resulting surface to form broad-scale vegetation community polygons.
2. 1 km Theme-buffer: Sites were buffered by a 1 km radius and the boundaries dissolved by attribute to form similar broad-scale vegetation community polygons.

Graphic representation of the TWINSPAN training sample point-feature interpolation and theme-buffer function were prepared.

Image classification

The vegetation community features of both the IDW interpolation and theme-buffer were used to create Areas of Interest (AOI) and subsequent community signatures in each Landsat ETM^+ image using ERDAS IMAGINE 8.6. These output signatures are representative of the reflectance or emission spectra related to vegetation and soil, forming different spectral signatures for different vegetation types. Two separate classifications viz. one using the IWD signatures and the other using the theme-buffer signatures were conducted under the maximum likelihood parametric rule, which assumes that the probability of a pixel belonging to a particular class is equal for all classes (ERDAS 1999).

The output-classified images were then converted to ArcGIS (ESRI 2004) grid data format and imported into ArcMap (ESRI 2004). A focal majority filter (Spatial Analyst), of 40x40 neighbour cells, was used to aggregate structural patterns and identify vegetation communities at a landscape scale. The *BoundaryClean* expression was then used to eliminate *NoData* cells, for a smoother surface. Subsequently, an omitted gabbro intrusion was on-screen digitized, using a 1:250 000 geological map backdrop.

Results and Discussion

The results of the TWINSPAN classification of 610 woody vegetation plots are presented as a dendrogram (Figure 2). The derived vegetation maps were compared to an independent test sample point data compiled by six reserve wardens within the study area using Kappa. The Kappa Statistic (Cohen 1960) was used to measure the agreement between predicted and observed categorizations of the data set, correcting for agreement that occurs by chance. The IDW interpolation (Figure 3) and theme-buffer classifications (Figure 4) yielded the following agreement for the Kappa statistic according to Fielding & Bell (1997) IDW $K = 0.37$ (poor) and theme-buffer $K = 0.56$ (good) with an overall accuracy of 0.52 ($p=0.05$) and 0.66 ($p=0.05$) respectively. The sample point buffer supervised classification of the Landsat ETM^+ imagery, consequently achieved a greater

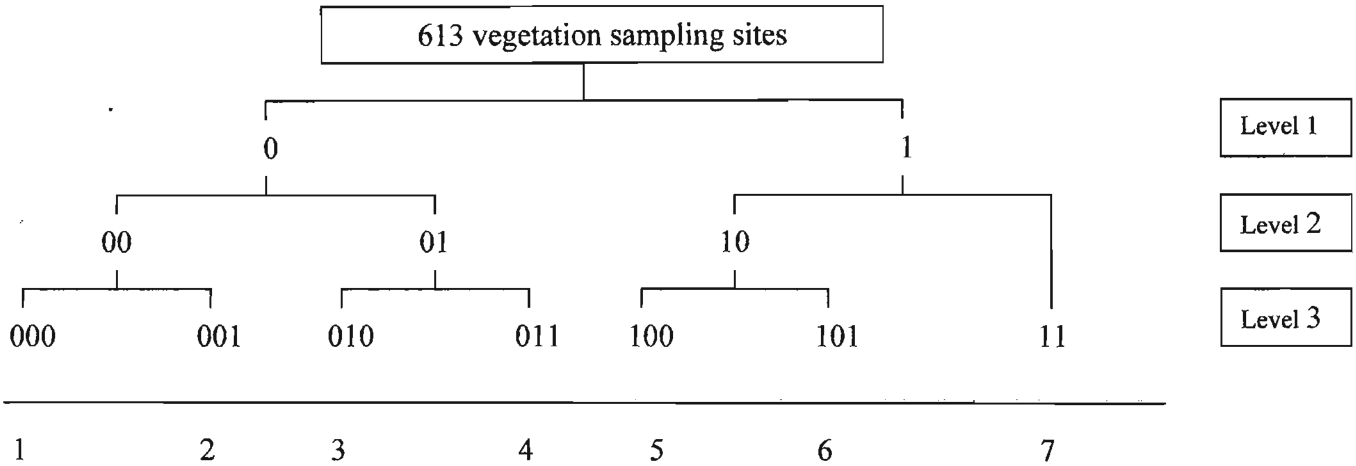


Figure 2 TWINSPAN dendrogram for 610 sites to the west of central Kruger National Park (see text for detail).

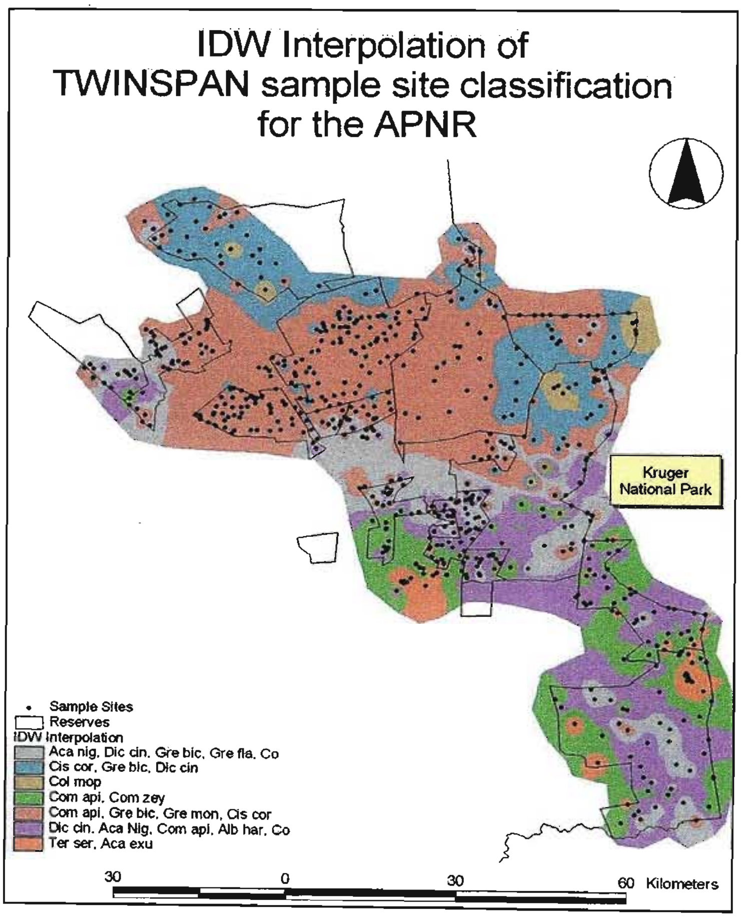


Figure 3 IDW interpolation of TWINSPAN sample site classification for the study area.

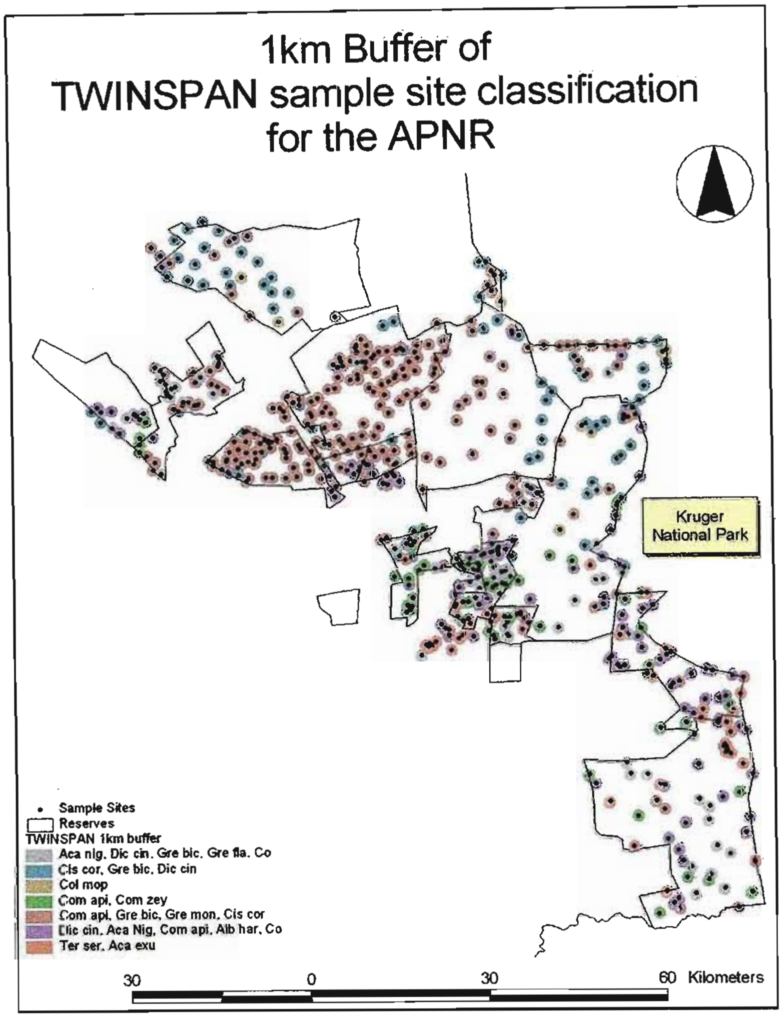
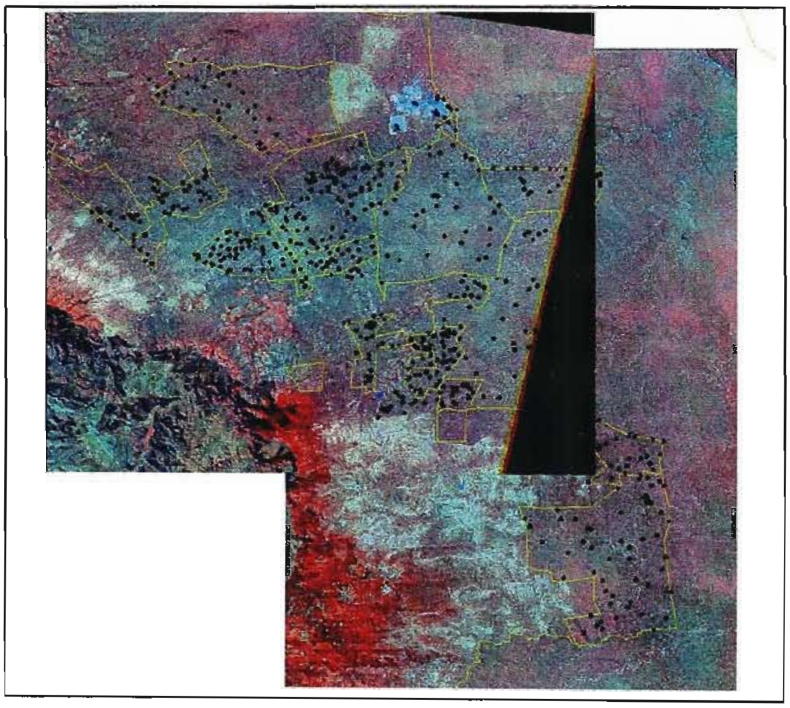


Figure 4 Sample Point Buffer of TWINSPAN sample site classification for the study area.

degree of accuracy than the interpolation method and the final vegetation map derived from this classification method was therefore accepted as the best representation of the vegetation communities of the study area (Figure 5).

A cross tabulation of the vegetation communities within the study area (Landsat/TWINSPAN) and the adjacent KNP (Landscapes, Gertenbach 1983) was completed (Table 1). This comparison was necessary to construct a map for the area to the west of the KNP that corresponds to that constructed for the KNP by Gertenbach (1983) and that constructed for the Limpopo National Park (LNP) in Mocambique (Stalmans *et al.* 2004) (Figure 6). This co-ordinated effort is essential for ecological monitoring purposes at a landscape scale across the APPAs, KNP LNP.



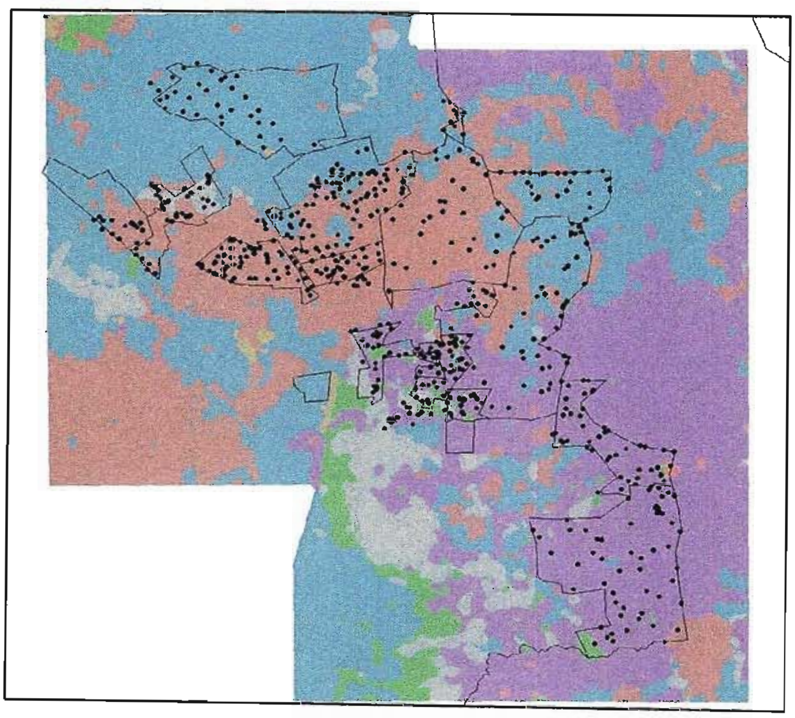


Figure 5 Landsat ETM+ (top) used for the Supervised Classification of the study area (bottom).

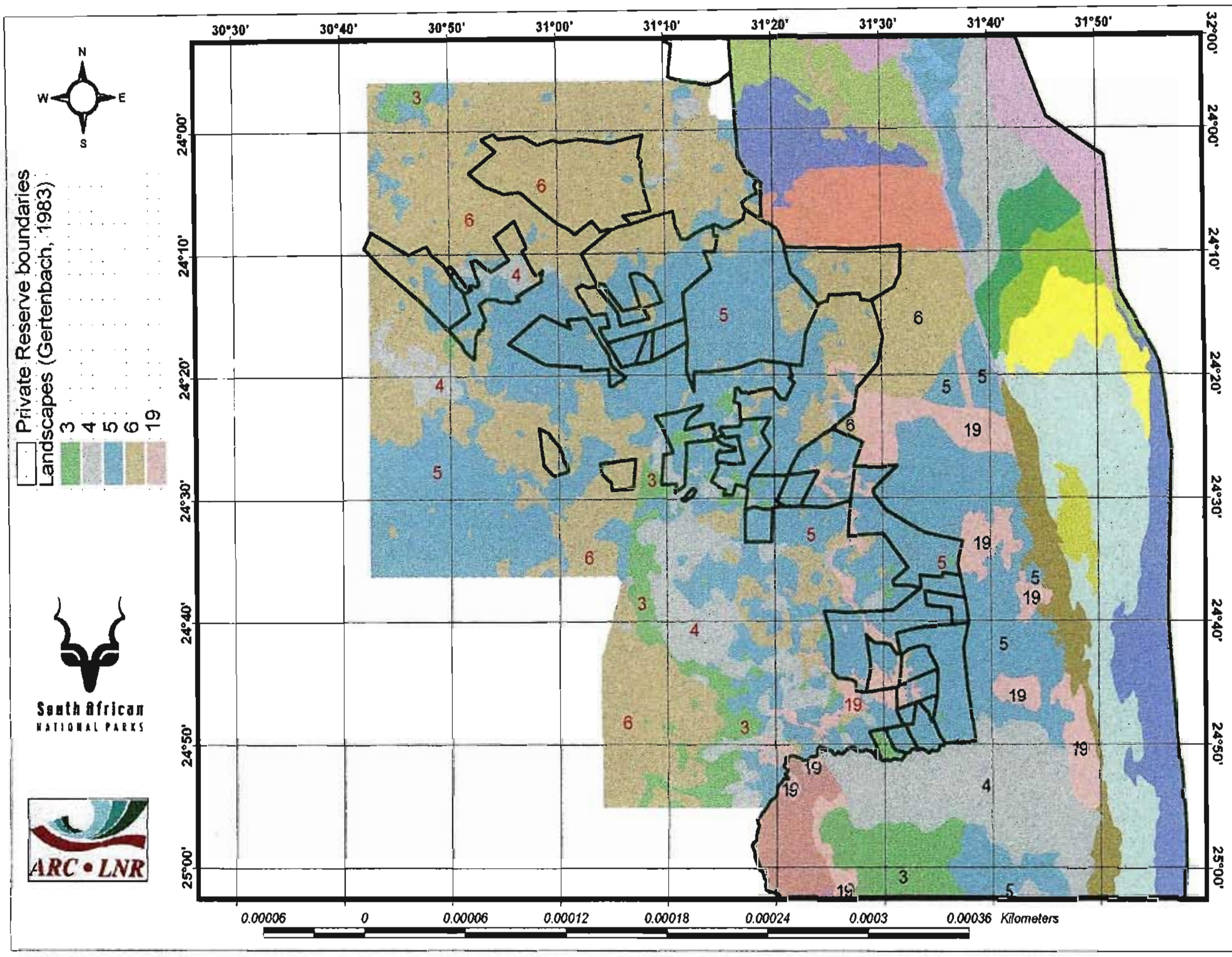


Figure 6 A landscape map for the area to the west of the KNP between the Sabie and Selati Rivers.

Table 1 A cross tabulation of the zones between the study area (Landsat/TWINSPAN) and KNP (Landscapes) classifications.

TWINSPAN	TWINSPAN_INDICATORS	LANDSCAPE	LANDSCAPE_DESCRIPTION
1	*Terminalia sericea* Low Closed Woodland	5	*Mixed Combretum* spp./ *Terminalia sericea* Woodland
3	*Albizia harveyii* Low Closed Woodland	5	*Mixed Combretum* spp./ *Terminalia sericea* Woodland
2	*Combretum zeyheri/Combretum apiculatum* Low Closed Woodland	3	*Combretum collinum / Combretum zeyheri* Woodland
4	*Acacia gerrardii/Combretum hereroense/Acacia exuvialis/Euclea divinorum* Low Closed Woodland	4	Thickets of the Sabie & Crocodile Rivers
5	*Combretum apiculatum/Grewia bicolor* Low Closed Woodland	6	*Combretum* spp./*Colophospermum mopane* Woodland of Timbavati
6	*Combretum apiculatum/Colophospermum mopane* Low Closed Woodland	6	*Combretum* spp./*Colophospermum mopane* Woodland of Timbavati
7	*Colophospermum mopane* Low Closed Woodland	6	*Combretum* spp./*Colophospermum mopane* Woodland of Timbavati
	Gabbro intrusion – derived from 1:250 000 geology	19	Thornveld on Gabbro

Woody plant communities and their location within the KNP Landscapes of Gertenbach (1983)

Plant Community 1: ***Terminalia sericea* Low Closed Woodland** and Plant Community 3: ***Albizia harveyi* Low Closed Woodland** forming part of Landscape 5 - **Mixed *Combretum* spp. – *Terminalia sericea* Woodland.**

Plant Communities 1 and 3 are found within the southern and central parts of the study area (Figure 6). In these areas, there are excellent examples of the soil catena that show the close correlation between soils and landforms and the role of water movement in hill slope processes (Tinley 1979; Venter 1986; Shahar 1990; Chappell 1992). The sequence from interfluve to drainage channel can be described as follows. Broad-leaved woody species and herbaceous layer dominated by moderate to low quality sandveld species, but containing elements of highly palatable productive perennial grasses characterize the sandy uplands. The hydromorphic midslopes are largely devoid of woody species but carry a dense moderate to low quality herbaceous layer. The duplex footslopes to alluvial valley bottoms support a largely microphyllous suite of woody species and a productive grass layer of high forage quality. The area is interspersed with numerous dolerite dykes.

Plant Community 1 represents the upland areas above the hydromorphic grasslands. The indicator species in this plant community are *Terminalia sericea* (frequency maximum (FM) = 69% and relative abundance (RA) >20%) and *Albizia harveyi* (FM = 67%; RA = 5 - 9%). *Terminalia sericea* dominates immediately above these grasslands with other broad-leaved woody species occurring higher up towards the crest of the slope. Species also classified as preferentials in this plant community include *Dichrostachys cinerea, Sclerocarya birrea, Gymnosporia heterophylla, Euclea divinorum, Peltophorum africanum, Phylenoptera capassa* and *Lannea scweinfurthii.* Additional species that occur with a FM of > 20% and RA > 10% include *Acacia exuvialis, Strychnos madagascariensis* and *Dalbergia melanoxylon.* Species with a wide distribution within this plant community include *Cissus cornifolia, Ormocarpum trichocarpum, Combretum zeyheri, C. collinum, C. apiculatum* and *Flueggea virosa.* The latter species generally occur at low RA with the exception of a small percentage of sites where *Combretum zeyheri* and *C. apiculatum* have RA's > 20%. The above agrees largely with the suite of woody species described by Gertenbach (1983) that occur on the deep upland sandy soils and the area immediately above the hydromorphic grasslands (seepline areas).

Physiognomically Plant Community 1 is characterized by Low Closed Woodland dominated by woodys within the 2 – 5 m height class and a mean crown: gap ratio of between 0.1 and 2ɵ as mean number of crown diameters apart (65% of the sites). This is in agreement with Gertenbach (1983) who describes the Landscape as having an upland area consisting of dense bush savanna vegetation. Other physiognomic classes in this plant community include Short Closed Woodland (2%), Tall Closed Woodland (2%), Low Open Woodland (17%), Low Sparse woodland (7%), Short Open Woodland (2%) and Tall Open Woodland (2%). The latter four classes are generally the result of bush control particularly in the southern parts of the study area.

Plant Community 3 represents the areas immediately below the hydromorphic grasslands with *Albizia harveyi* (FM = 45%; RA = 10-19%) as the indicator species. Species also classified as preferentials within this plant community include *Cissus cornifolia, Lannea scweinfurthii* and *Peltophorum africanum*. Additional species that occur with an FM > 20% and RA > 10% include *Ormocarpum trichocarpum, Acacia exuvialis, Grewia monticola, Dichrostachys cinerea, Dalbergia melanoxylon, Combretum hereroense, C. apiculatum* and *Acacia gerardii.* Species with a wide distribution within this plant community include *Acacia nigrescens, Ziziphus mucronata, Gymnosporia heterophylla, Grewia monticola, G. bicolor, Commiphora schimperi,* and *Protasparagus* spp.. The latter species generally occur at low RA with the exception of a small percentage of sites where *Gymnosporia heterophylla, Euclea divinorum, Grewia bicolor* and *Acacia nigrescens* have RA's > 20%. All of the above species are included in Gertenbach's (1983) description of the bottomland areas.

Physiognomically Plant Community 3 is characterized by Low Closed Woodland as described above (66% of the sites). Other physiognomic classes in this plant community include Short Closed Woodland (2%), Low Open Woodland (15%), Low Sparse Woodland (10%), Short Open Woodland (1%), Tall Open Woodland (1%), Tall Sparse Woodland (1%), Low Thicket (2%), Low Closed Grassland (1%) and Short Closed Grassland (1%). The open and sparse woodlands and grassland areas are generally the result of bush control and follow-up management that maintain this physiology.

Plant Community 2: ***Combretum zeyheri/C. apiculatum* Low Closed Woodland** forming part of Landscape 3 – ***Combretum collinum/C. zeyheri* Woodland**

As with Plant Communities 1 and 3, Plant Community 2 occurs within the southern and central parts of the study area (Figure 6). *Combretum zeyheri* (FM = 66%; RA > 20%), *C. apiculatum* (FM = 66%; RA > 20%), *Pterocarpus rotundifolius* (FM = 55%; RA > 20%) and *Grewia flavescens* (FM = 34%; RA = 5-9%) are the indicator woody species in this community. This upland community occurs in areas with good internal drainage and consists of a broad-leaved plant community with a herbaceous layer dominated by moderate to low quality sandveld species, but containing elements of highly palatable productive grasses. The area is also interspersed with numerous dolerite dykes. Species also classified as preferentials in this community include *Grewia monticola, G. bicolor, Acacia nigrescens, Ozoroa engleri,* and *Commiphora schimperi.* Additional species that occur with an FM > 20% and RA > 10% include *Strychnos madagascariensis, Dalbergia melanoxylon* and *Acacia exuvialis.* Species with a wide distribution within this plant community include *Cissus cornifolia, Acacia exuvialis, Terminalia sericea, Albizia harveyi, Ormocarpum trichocarpum, Dichrostachys cinerea, Combretum collinum, Flueggea virosa, Sclerocarya birrea* and *Acacia gerrardii.* The latter species generally occur at low RA with the exception of a small percentage of sites where dense patches of *Terminalia sericea* occur at RA > 20%. The above agrees largely with the suite of woody species described by Gertenbach (1983) that occur on the deep sandy upland soils and the area immediately above the hydromorphic grasslands (seepline areas). Species such as *Acacia gerrardii* and A. *nigrescens* are more common just below the seeplines and in the bottomlands respectively.

Physiognomically Plant Community 2 is characterized by Low Closed Woodland. (77% of the sites). This is in agreement with Gertenbach (1983) who describes the uplands of this Landscape as consisting of dense bush savanna between 1 and 5 m in height. Other physiognomic classes in this plant community include Tall Closed

Woodland (4%), Low Open Woodland (13%), Low Sparse woodland (2%), Short Open Woodland (2%), Low Thicket (2%).

In conclusion, it is apparent that this Landscape forms discrete units within the larger Landscape 5. The relatively low proportions of *Combretum collinum* within the study area concurs with van Wyk (1984) who states that this species, although widespread in west of the KNP and APPAs is only abundant in the Pretoriuskop/Malelane and Punda Maria areas.

Plant Community 4: ***Acacia gerrardii/Combretum hereroense/Acacia exuvialis/Euclea divinorum* Low Closed Woodland** forming part of Landscape 4 – **Thickets of the Sabie and Crocodile Rivers**

Plant Community 4 occurs in small pockets in generally lower-lying areas throughout the study area. The structure of the vegetation, described as 'a dense woody vegetation' (Gertenbach (1983) is important in this community with elements occurring along the Timbavati, Klaserie, Olifants and Makhutswi Rivers. There are two variations identified within the study area, one associated with brack (sodium saturated) soils in the lower-lying areas and the other with dolerite intrusions with darker soils. The herbaceous layer in the brack areas is high in sodium and susceptible to overgrazing resulting in a generally sparse field layer, particularly near artificial water points where large numbers of grazing animals are present. In the dolerite areas, the grass cover is generally higher with robust species such as *Themeda triandra* dominating.

Gymnosporia heterophylla (FM = 49%; RA > 20%), *Grewia flavescens* (FM = 57%; RA = 10-19%), *Flueggea virosa* (FM = 47%; RA = 10-19%), *Ehretia rigida* (FM = 46%; RA = 10-19%) and *Grewia bicolor* (FM = 57%; RA = > 20%) are the indicator species within Plant Community 4. Species also classified as preferentials within this plant community include *Euclea divinorum, Combretum hereroense, Acacia nigrescens, Ziziphus mucronata, Rhus gueinzii* and *Gardenia volkensii*. Additional species that occur with an FM > 20% and RA > 10% include *Acacia exuvialis, A. gerrardii, Combretum apiculatum, C. hereroense, Dalbergia melanoxylon, Dichrostachys cinerea, Grewia monticola* and *Ormocarpum trichocarpum*. Species with a wide distribution within this plant community include *Albizia harveyi, Phylenoptera capassa, Commiphora schimperi, Protasparagus* spp., *Cissus cornifolia* and *Sclerocarya birrea*. The latter species generally occur at low RA. The plant communities described in Landscape 4 correspond largely with the bottomland vegetation in Landscapes 3 and 5 described above. This concurs with the results of Gertenbach (1983) in terms of the woody species that occur on the brack (sodium saturated) soils in the bottomland areas and the other associated with dolerite intrusions with darker soils.

Physiognomically Plant Community 4 is characterized by Low Closed Woodland (64% of the sites). This is in agreement with Gertenbach (1983) who describes this landscape being characterized by dense woody vegetation. Other physiognomic classes in this plant community include Low Open Woodland (20%), Low Sparse woodland (4%), Short Open Woodland (3%), Short Closed Woodland (4%), Tall Sparse Woodland (1%), Low Thicket (3%) and Low Closed Grassland (1%).

Plant Community 5: ***Combretum apiculatum/Grewia bicolor* Low Closed Woodland**, Plant Community 6**: *Combretum apiculatum/Colophospermum mopane* Low Closed Woodland** and Plant Community 7: ***Colophospermum mopane* Low Closed Woodland** forming part of Landscape 6 - ***Combretum* spp./*Colophospermum mopane* Woodland of the Timbavati area**

Plant communities 5 to 7 predominate in the northern parts of the study area corresponding with Landscape 6 (***Combretum* spp./*Colophospermum mopane* Woodland of the Timbavati area**). The northern part of the study area is gently undulating to flat, with frequent doleritic intrusions (Witkowski 1983; Scholes 1987; Walraven 1989). The catenary sequence that develops on granite-derived soils in the Lowveld is visible in the southern parts of these northern areas and there is a tendency towards sodicity and duplex soils in the bottomlands. The soils in the north tend to be shallower and are less differentiated than the southern areas, showing no catenary sequence (Scholes 1987). The vegetation is very mixed in these areas containing both broad-leaved and microphyllous elements but with *Colophospermum mopane* generally dominating the woody layer. The grass layer is generally sparser than in the south, containing a mixture of palatable productive and unpalatable species.

The ***Combretum apiculatum/Grewia bicolor* Low Closed Woodland** (Plant community 5) represents the upland areas on granite and gneiss in the southern part of Landscape 6 (Gertenbach 1983) (Figure 6). The indicator species in this plant community are *Grewia bicolor* (FM = 42%; RA = > 20%) and *G. hexamita* (FM = 36%; RA = 2-4%). *Combretum apiculatum* (FM = 85%; RA > 20%) and *Grewia bicolor* dominate this plant community. Species also classified as preferentials within this plant community include *Dichrostachys cinerea, Acacia nigrescens, Terminalia prunoides* and *Grewia villosa.* Additional species that occur with an FM > 20% and RA > 10% include *Cissus cornifolia* and *Grewia monticola.* Species with a patchy distribution within this plant community include *Acacia exuvialis, A. nigrescens, Boscia albitrunca, Commiphora mollis, C. schimperi, Grewia flavescens, Protasparagus* spp., *Sclerocarya birrea*, *Commiphora pyracanthoides* and *Lannea schweinfurthii.* The latter species generally occur at low RA with the exception of a small percentage of sites where dense patches of *Colophospermum mopane* occur at RA > 20%.

Physiognomically Plant Community 5 is characterized by Low Closed Woodland (76% of the sites). Other physiognomic classes in this plant community include Short Closed Woodland (1%), Tall Closed Woodland (0.5%), Low Open Woodland (14%), and Low Sparse woodland (5%), Short Open Woodland (1%), Tall Open Woodland (1%), Low Thicket (1%), Low Closed Grassland (0.5%) and Low Open Grassland (0.5%).

The ***Combretum apiculatum/Colophospermum mopane* Low Closed Woodland** (Plant community 6) is found in the northern parts of the study area and illustrates the relationship described by Gertenbach (1983) where *Combretum apiculatum* (FM = 84%; RA = > 20%) dominates in the sandy areas and *Colophospermum mopane* (FM = 65%; RA > 20%) the clay areas. The indicator species in this plant community are *Colophospermum mopane* and *Dalbergia melanoxylon* (FM = 53%; RA = 2-4%). Species also classified as preferentials within this plant community include *Ormocarpum trichocarpum* and *Lannea schweinfurthii.* Additional species that occur with an FM > 20% and RA > 10% include *Grewia bicolor, G. monticola* and *Cissus cornifolia.* Species with a wide distribution within this plant community include *Boscia albitrunca, Protasparagus* spp., *Dichrostachys cinerea, Acacia nigrescens, Sclerocarya birrea,* *Grewia flavescens, Commiphora schimperi, C. pyracanthoides* and *C. mollis.* The latter species generally occur at low RA.

Physiognomically Plant Community 6 is characterized by Low Closed Woodland (75% of the sites). Other physiognomic classes in this plant community include Short Closed Woodland (1%), Tall Closed Woodland (1%), Low Open Woodland (12%), Low Sparse woodland (9%), Low Open Grassland (1%) and Low Sparse Grassland (1%).

Plant Community 7 is described as ***Colophospermum mopane*** **Low Closed Woodland**. This community is dominated exclusively by *Colophospermum mopane* (FM = 100%; RA > 20%). The indicator species in this plant community is *Acacia exuvialis* (FM = 100%; RA = 10-19%). In the higher clay areas species classified as preferentials include *Rhigozum zambesiacum, Dalbergia melanoxylon, Combretum apiculatum,* while on sandy areas preferentials include *Boscia albitrunca, Grewia bicolor* and *Protasparagus* spp..

Physiognomically Plant Community 7 is characterized by Low Closed Woodland. Other physiognomic classes in this plant community include, Low Open Woodland (25%), Low Sparse woodland (8%), Low Closed Grassland (8%) and Short Closed Grassland (8%).

Plant Communities 5 and 6 show a large degree of overlap of woody species described for Landscape 6 which is in turn similar to the previously discussed Landscape 5 but for the absence of *Combretum zeyheri* (Gertenbach 1983). Physiognomically, however, the Low Closed Woodland classification ascribed to this part of the study area differs from that of Gertenbach (1983) who describes the Landscape as being an open bush savanna.

Plant Community: ***Thornveld on Gabbro*** (Gertenbach 1983)

This plant community, while not formally isolated in this study, runs in a thin band from the central part of the study area southwards. The landscape is generally located at a higher altitude than the surrounding granite (Gertenbach 1983). Three variations are described by Gertenbach that occur in the study area, an *Acacia nigrescens* shrubveld on shallower soils in the central-northern areas, an *Acacia nigrescens/Sclerocarya birrea* element on deeper soils, and a *Lannea schweinfurthii/Pterocarpus rotundifolius* community in the southern part of the study area.

Physiognomically, by physical observation done during the annual aerial game counts, this plant community has elements that vary from Low Open Grassland through Low Open and Closed Shrubland and Woodland through Short and Tall Open Woodland.

The seven plant communities identified in the current study were thus satisfactorily accommodated within various topographical units of the four extrapolated Landscapes (Figure 6). This contribution thus links to the co-ordinated effort extending into the Trans-Frontier National Park in Mocambique, and specifically to the work done by Gertenbach (1983) and Stalmans *et al.* (2004).

Issues of ecological importance within the woody plant communities of various Landscapes

Plant Community 1: ***Terminalia sericea* Low Closed Woodland** and Plant Community 3: ***Albizia harveyi* Low Closed Woodland** forming part of Landscape 5 - **Mixed *Combretum* spp. – *Terminalia sericea* Woodland**

Plant Community 1 is ecologically important for, among other reasons, the *Terminalia sericea* band that forms a Low Closed Woodland 'fringe' around the hillslope that provides shelter for prey species such as blue wildebeest (*Connochaetes taurinus*). The latter feed preferentially in the more open short-grass bottomlands and seek shelter in the more densely vegetated upslopes as described above. It is postulated that extensive clearing of the entire slope for improved wildlife visibility for tourism in some protected areas has removed this critical shelter to the detriment of prey species and to the benefit of predators such as lion (*Panthera leo*). This is illustrated by Peel (2002; 2003) who shows the effect of lion predation on wildebeest in areas where that habitat has been extensively manipulated.

Of ecological importance is the contrast between the physiognomic classification in the current study that classifies Plant Community 3 as a Low Closed Woodland and that of Gertenbach (1983) who described this part of the landscape as a generally open tree savanna. These bottomlands consist of sensitive calc-brack clays or dark grey skeletal, sandy, often stony, excessively drained soils (Tinley 1979) prone to erosion patterns associated with hillslope hydrology and soil erodibility factors (Chappell 1992). Sodic site erosion is related to subsurface water flow and reduced soil strength above the junction of the permeable A-horizon and the impermeable B-horizon (Chappell 1992). Sodium descending the slope plays a key role by causing deflocculation of the clay fraction. The resulting non-aggregated soil is vulnerable to displacement by moving water and erosion. The situation is exacerbated by the attractiveness of the grazing in these base saturated, sodium dominated soils. Injudicious management practices such as the provision of artificial water points, result in excessive grazing and poor soil moisture conditions in these sensitive areas. Further, poorly placed roads and tracks act as waterways, with water run-off channeled directly into drainage lines 'drying out' these sensitive bottomland areas. The latter, with poor placement of water points and heavy grazing in many of these sodic areas, results in a loss of top soil, reduced ability of the grass layer to compete with the deeper-rooted woody layer, diminished grass cover, extensive areas of accelerated soil erosion and ultimately bush encroachment.

Plant Community 4: ***Acacia gerrardii/Combretum hereroense/Acacia exuvialis/Euclea divinorum* Low Closed Woodland** forming part of Landscape 4 – **Thickets of the Sabie and Crocodile Rivers**

The discussion presented for Plant Community 3 for sodic areas is also relevant to Plant Community 4.

Plant Community 5: ***Combretum apiculatum/Grewia bicolor* Low Closed Woodland**, Plant Community 6**: *Combretum apiculatum/Colophospermum mopane* Low Closed Woodland** and Plant Community 7: ***Colophospermum mopane* Low Closed Woodland** forming part of Landscape 6 - ***Combretum* spp./*Colophospermum mopane* Woodland of the Timbavati area**

Ecologically, *Colophospermum mopane* provides the key habitat for some of the rare species of the KNP, viz. Roan antelope (*Hippotragus equinus*), Sable antelope (*H. niger*) and Tsessebe (*Damaliscus lunatus*) (Kennedy & Potgieter 2003). *Colophospermum mopane* is also an important browse resource, with the leaves particularly sought after in times of drought. *Colophospermum mopane* faces a number of threats outside of protected areas. These include clearing land for agricultural purposes and harvesting of fuelwood and building materials for rural communities. *Colophospermum mopane* is also a primary host for the Mopane Worm (*Imbrasia belina*) the larvae of which is widely used as a food source in north-eastern South Africa, Mocambique, Malawi, southern Zimbabwe, north-eastern Botswana, Namibia and Zambia (Greyling & Potgieter 2004). The commercial value of *I. belina* further demands the sustainable management of Mopane woodlands.

Plant Community: ***Thornveld on Gabbro*** (Gertenbach 1983)

Ecologically this area performs an important function in that it is generally dominated by the grass *Themeda triandra* that is palatable when young but which loses palatability and is poorly utilized when mature on this soil type. In early spring, the new shoots of *Themeda triandra* are palatable particularly after burning. Judicious burning can therefore be used as a management tool to attract game onto these areas thus releasing grazing pressure on the surrounding granitic areas. Due to the relative unpalatability of the grass layer at the end of winter particularly in the higher rainfall southern part of the study area, fuel loads are high and frequent hot fires result in a stunted tree layer with few large trees. In the Sabi Sand Wildtuin extensive bush control has exacerbated the situation resulting in sparse woodland. Added to this, the influx of elephant from the

KNP since the removal of the boundary fence between these two areas in 1993 has resulted in the destruction of many of the remaining adult *Acacia nigrescens* trees.

General

A comparison of the 1944 and 1986 aerial photographs of the eastern Lowveld exhibit a pattern of increasing woody plant density and changed structure over extensive areas (Peel *et al.* 2004). This concurs with the physiognomic assessment done by Gertenbach (1983) which, while not detailed, corresponds largely with the objectively obtained results of the current study which points to a thickening up of the woody component and homogenisation in structure. The cause of these changes occurs at two scales, a relatively small scale (lower level environment and management) and a larger scale (higher level or atmospheric). The former, in conjunction with increasingly variable environmental conditions includes injudicious management such as poor road placement, heavy grazing and a concomitant reduction in fire resulting in an opening up of space where tree seedlings can germinate in the absence of competition from grass. Resulting conditions are not optimal for the grazing species that, because of their dominance in the Lowveld savannas, are critical to wildlife operations. At the higher level, contributors to bush encroachment include the impact of elevated CO_2 levels in the atmosphere on tree: grass interactions. Bond et al. (2003) simulated the effects of increases in CO_2 from pre-industrial times to the present and found large increases in tree density driven by CO_2 fertilisation of tree growth. The latter suggests that increasing CO_2 levels in the atmosphere may in part, drive bush encroachment in savanna areas.

Physiognomically the contrast between the current study which classifies Plant Community 3 as a Low Closed Woodland and that of Gertenbach (1983) who described this part of the landscape as a generally open tree savanna is important. These bottomlands consist of sensitive calc-brack clays or dark grey skeletal, sandy, often stony, excessively drained soils (Tinley 1979) prone to erosion patterns associated with hillslope hydrology and soil erodibility factors (Chappell 1992). Sodic site erosion is related to subsurface water flow and reduced soil strength above the junction of the permeable A-horizon and the impermeable B-horizon (Chappell 1992). Sodium descending the slope plays a key role by causing deflocculation of the clay fraction. The resulting non-aggregated soil is vulnerable to displacement by moving water and erosion. The situation is exacerbated by the attractiveness of the grazing in these base saturated, sodium dominated soils. Injudicious management practices such as the provision of artificial water points result in excessive grazing and poor soil moisture conditions in these sensitive areas. Further, poorly placed roads and tracks act as waterways, with water run-off directly into drainage lines 'drying out' these sensitive bottomland areas. The latter, with poor placement of water points and heavy grazing in many of these sodic areas, results in a loss of top soil, reduced ability of the grass layer to compete with the deeper-rooted woody layer, diminished grass cover, extensive areas of accelerated soil erosion and ultimately bush encroachment.

Savannas make up some 34% of the land surface of South Africa and indeed some 40% of the land surface of Africa and are second only to tropical forests in their contribution to primary production (Scholes & Walker 1993). They also make up a substantial organic carbon pool that will be an important source or sink for atmospheric carbon dioxide in the future (Scholes & Walker 1993). Further, savannas are home to most of the human population and form the basis of both the wildlife and cattle industries in Africa. It is therefore critical that we assess the ecological potential and current condition of extensive savanna areas at least at a landscape scale to achieve the objective of gaining a predictive understanding of savanna vegetation dynamics. The combination of satellite imagery and objectively collected field data was satisfactorily employed to set up a classification of areas into functionally similar landscapes while allowing for up and downscaling. The findings of this study therefore allow us to compare critical response variables under similar environmental and woody vegetation conditions but with different management regimes. The technique thus has the potential for use in other African savannas.

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Chapter 4

The evolving use of indices currently based on animal number and type in semi-arid heterogenous landscapes and complex land-use systems

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Abstract

Methods of determining animal numbers (stocking rate) based on metabolic mass, animal type and biomass are reviewed in the context of equilibrial/disequilibrial paradigms. In South Africa, the calculation of 'carrying capacity' is based on conversion of animal species to metabolic mass equivalents. This assumes homogenous systems which tend to some point of equilibrium. It is applied widely in commercial livestock systems involving one or two species. Examination of a case study in the Lowveld of the Northern Province, South Africa, showed that the determination of 'stocking rate', based on metabolic mass, in this multi-herbivore and heterogenous system, overestimated the 'carrying capacity' of the reserve over 20 years. The actual animal numbers in the system dropped by c. 4 000 kg km^{-2} after a drought in the early period of the study into the bounds as determined by a model incorporating rainfall and animal biomass. An approach to determine stocking density using animal type, biomass, rainfall and vegetation parameters is suggested. The development of this as a coarse-scale (regional) and ranch-specific model to cover a range of scales and heterogeneity in key resources is advocated.

Additional index words: animal biomass, animal type, carrying capacity, stocking density, stocking rate.

Introduction

In its essence the notion of 'carrying capacity', and to an extent the related indices 'grazing capacity' and 'stocking rate', presupposes a sufficiently homogenous system with a known or supposed optimal point of 'stability' based on equilibrium theory, non-deterioration of vegetation or soil over an extended term, and a land use objective of maximum animal production (Danckwerts 1982a; Trollope *et al.* 1990;). Trollope *et al.* (1990) first express 'carrying capacity' as ha AU^{-1} (Animal Unit – defined as an animal with a mass of 450kg which gains 0.5kg per day on forage with a digestible energy percentage of 55% (Trollope *et al.* 1990) - or AU ha^{-1}), later dividing the term into 'Grazing/Browsing Capacity' based on the fact that there are both grazeable and browseable components to the vegetation. The original 'carrying capacity' concept is advanced by the introduction of an economic element and the term 'economic carrying capacity' (Caughley 1979; Danckwerts 1982a). A related term defines 'ecological carrying capacity' (often used as a yardstick in ecotourism) as the population size of an organism in an area as determined by the capacity of that area to support the individuals in that population and enable them to reproduce (Caughley 1979; Grossman 1984).

Ecosystem functioning in African savannas has been variously described along a stable (equilibrium) - unstable (disequilibrium) continuum. 'Stable state' thinking as described above, while still obviously useful and widely applied in commercial agriculture, has been aggressively challenged by the disequilibrium school, espoused at very developed levels in Behnke *et al.* (1993). Two of the more extreme claims made by Behnke *et al.* (1993), are that there is no central tendency (point of equilibrium) operating in these systems, and that plant and animal dynamics are uncoupled (changes in rainfall causing population declines before herbivores can influence rangelands deleteriously).

This shift in thinking is attributed to the fact that arid and semi-arid African environments are heterogenous, highly changeable and complex, rather than homogenous, Clementsian in progression and culminating in a stable climax community. Under such conditions, Behnke *et al.* (1993) claim that carrying capacity notions, as described in Danckwerts & Stuart-Hill (undated), and defined by Caughley (1979), Danckwerts (1982a), Grossman (1984) and Trollope *et al.* (1990) are inappropriate.

These claims have been challenged by Illius & O'Connor (1998) (citing examples given by the original authors), but are considered to have had a wholesome effect on the rangeland science discipline in Africa in that they have focussed on the importance of resource heterogeneity.

Sadly, recommendations to policy makers in South Africa have been unduly influenced, at least at the implementation level, by this disequilibrial thinking, as indeed they were by the carrying capacity notion (Anon. 1998). Realistic decision-making should take place in the framework which more closely models the actual key parameters and processes in African rangelands, rather than some ideological '-ism' of near perfect or totally non-existent equilibrium.

Ecosystem theories

Ideas of a number of theories pertaining to the description of ecosystems along an equilibrium/disequilibrium continuum can be summarised in terms of their basic tenets (Table 1).

Scale and heterogeneity

The spatial and temporal scale at which conservation areas are managed influences the extent to which the stability-based suite of indicators might be used. Spatial and temporal heterogeneity at different scales are prime determinants of system qualities. Heterogeneity is an important consideration in any operation based on the use of natural resources, for example, the Kruger National Park (KNP - *c.* 2 000 000 ha) has adopted the Noss (1990), definition of biodiversity as an underlying basis for their revised management plan (Braack 1997a; Braack 1997b) which is expressed operationally in terms of so-called 'thresholds of potential concern', endpoints of which even include the desirability of having a certain limited percentage of land in a 'degraded' condition for a period of time due to biodiversity considerations. Large adjacent private nature reserves (varying from 20 000 ha to 90 000 ha) which have embraced the basic philosophies of the KNP management plan since the removal of the fence between them, have similar general objectives but on different spatial scales. Small fenced reserves and ranches (up to 10 000 ha) to the west of the large reserves (intermediate scale), where little or no movement is possible have similar objectives but, due to their size, present a unique set of management challenges. In the latter case 'island populations' undergo more extreme eruptions in numbers and related vegetation over-utilisation than in larger systems (Owen Smith 1983).

The degree of management required depends on the scale of interest. **Small scale vegetation heterogeneity** is illustrated by Belsky (1988) who isolated patches which ranged in width from 0.5 to 10.0 m and in intensity from simple differences in species abundances to

Table 1 A description of ecosystem theories and principles.

Theory	Basic principles and examples	Referenced examples
1. Equilibrium	Plant succession; Climate driven; Monoclimax vegetation	Clements (1916)
	Plant succession; Climate driven; Polyclimax (edaphic); Disturbance influence (e.g. heavy grazing)	Gleason (1926); Tansley (1935)
2. Stable equilibrium	Return to equilibrium following deflection; Elephants determine structure and dynamics of the woody layer; Elephants are not the ultimate cause of woody declines; There is stability in the elephant/tree interaction; On the eastern plains of Serengeti it is shown that the degree of wildebeest feeding on the grass layer is not great enough to destabilise the plant-herbivore interaction;	 Laws (1970) Croze (1974a,b); Croze *et al.* 1981) Sinclair *et al.* (1985)
	Fire Hypothesis - Fire causes woody mortality and prevents regeneration of small trees; Reduction in fire frequency results in a return to woodland (elephant impact incidental)	Norton-Griffiths (1979)
3. Multi-directional succession	Not classical succession; Occurs over a range of temporal scales; Confounded by non-directional changes; Precursor of Multiple Stable State (MSS) theory	Walker (1980)
4. Multiple Stable State (MSS) theory	Several stable vegetation types exist; For e.g. the existence of two equilibria - many trees and few elephants and many elephants and few trees; Reduce elephants and fire for trees to regenerate	Dublin (1995)
5. Multi-disclimax communities	Multiple stable points in the same locality; Alternative to Clements's (1916) theory of a climate driven climax for every region	Belsky (1986)

(Table 1 continued overleaf)

6. Cyclic models - Stable Limit Cycle	Biota are continuously moving between phases of a cycle; Differs from MSS in that it suggests woodland ecosystems containing elephants can never reach a natural stable equilibrium; Elephants alone will not cause a decline in the tree population because before this happens elephants will die-off or emigrate	Caughley (1976)
7. Non-equilibrium theory	Implies some degree of destabilisation of the resource by abiotic and/or biotic factors to the detriment of the biotic component, e.g. unstable plant/herbivore interactions; e.g. woodlands in the Serengeti would disappear due to over-utilisation by elephant; e.g. an increase in unpalatable and ungrazed grasses during periods of high wildebeest density in the Serengeti; If the resource deteriorates to a point where large scale mortality occurs, would this be followed by a period of vegetation recovery and a subsequent increase in the animal component? If so then non-equilibrium as presented here could simply be described as a phase in a long term equilibrium scenario	McNaughton (1983) Sinclair (1995)
8. Disequilibrium	There is no equilibrium operating in these systems; Plant/herbivore dynamics are uncoupled, with dry periods (rainfall) causing herbivore population declines before they can influence the vegetation component deleteriously; The claims by Behnke *et al.* (1993) have forced rangeland scientists to consider resource heterogeneity as opposed to stability theory (which assumes homogeneity); Their claims have been shown to be questionable.	Behnke *et al.* (1993) Illius & O'Connor (1998)

compositionally distinct mosaics. At an intermediate scale, McNaughton & Banyikwa (1995) found little or no correlation in green biomass among three sites, separated by a distance of 3-10 km, in the Serengeti ecosystem.

At a ranch scale Danckwerts (1989), using data gathered for the False Thornveld of the Eastern Cape, attempted to predict grazing capacity in terms of range condition and rainfall. His results showed enormous variation even on the same property, indicating that although we may predict the correct average grazing capacity, some areas will remain understocked and some areas, so called 'hot spots', will be overstocked. He showed that, for a ten year period, in only 2 years out of the 10 did the grazing capacity fall within a range of 25% on either side of the long term mean grazing capacity. Herbivores therefore encounter a constantly shifting mosaic of production, which is driven by variable rainfall (McNaughton & Banyikwa 1995). In domestic systems this can be masked by short-term (3-6 monthly) adjustments to animal numbers based on previous rainfall (Danckwerts 1982b). The rapid manipulation of the numbers of wild herbivores presents logistical problems in terms of fecundity and marketing.

Landscape pattern

Pattern generated by processes operating at different scales results in landscape formation (Urban *et al.* 1987). Urban *et al.* (1987) suggest that the multi-levelled organisation of landscapes be looked at in terms of a hierarchy theory whose organised systems can be broken into discrete functional components operating at different scales.

A hierarchical perspective emphasises three strategic concerns in landscape pattern analysis (Urban *et al.* 1987):

(1) to detect pattern and define its spatial and temporal scale, i.e. define functional patches at a certain level;

(2) to infer which factors generate the pattern (critical building blocks); and

(3) relate this pattern to adjacent levels.

An important scale related issue is whether an area, given a particular disturbance, is large enough to tolerate such disturbance? (Urban *et al.* 1987). A landscape which is unable to incorporate a disturbance has a transient frequency distribution of patch types which changes in response to each disturbance event and is termed a **non-equilibrating landscape** (Urban *et al.* 1987). Conversely, a landscape, large enough to incorporate the factors that disturb its component patches, has a constant frequency distribution of patches of all types at all times and is termed an **equilibrating** landscape. Related to the above, is **anthropogenic rescaling** where man rescales patterns in time and space (Urban *et al.* 1987). Anthropogenic scaling has the effect of:

(1) rendering natural incorporating mechanisms less effective;

(2) changing the set of constraints (including disturbance frequencies) governing lower level biotic processes; and

(3) changing the degree of interaction among patches, and therefore altering behaviour which may influence higher level processes (Urban *et al.* 1987).

The concepts of equilibrating and non-equilibrating landscapes, as well as anthropogenic rescaling are well illustrated in the savanna areas of the Lowveld of South Africa. Man has manipulated animal and plant communities by compressing them into small fenced areas, providing them with water and, in some cases, providing them with supplementary feed. This has altered fire regimes, the type and number of animals which can be kept, which in turn leads to a homogenisation of vegetation structure, composition, productivity and ultimately carrying capacity (large equilibrating systems have been anthropogenically rescaled to non-equilibrating systems).

Urban *et al.* (1987) suggest that areas of small- to intermediate- scale which cannot incorporate their internal dynamics (non-equilibrating landscapes), can be equilibrated by rescaling their internal dynamics to effect smaller patches. In intermediate scale areas to the west of the Kruger National Park for example, structured animal manipulation may be used to promote limited fluctuations in response to varying vegetation conditions while not permitting large scale mortality. Another approach could be to use fire opportunistically in smaller areas, thus allowing for the use of fire in an area which would not contain a wildfire. Fenced areas, managed in isolation (man-dominated), provide empirical observations from which to deduce critical thresholds of interaction among components and give us insights into the use of ecological scaling.

Animal type and feeding class

There are two different forage sources in grass/bush communities, namely, graze and browse. These forage sources are utilized separately by grazers and browsers although there is some overlap between them. The carrying capacity of an area is taken as the sum of its grazing and browsing capacities (Danckwerts & Stuart-Hill undated). The exact diets of animals are debatable and the point of their division arbitrary. The Large Stock Unit (LSU - see Animal Unit definition above), Grazer Unit (GU – the metabolic equivalent of a grazing animal with a mass of 180 kg) and Browser Unit (BU – the metabolic equivalent of a kudu with a mass of 140 kg) approaches however, require that mixed feeders be apportioned between grazers and browsers according to diet (Peel *et al.* 1991; Dekker 1997). The latter method results in the impact of species within the mixed feeder class being under emphasised. The following guidelines regarding the percentage of grazers, browsers and mixed feeding classes were considered. Mentis & Duke (1976) suggested a ratio of non-selective grazers to selective grazers to browsers of 40%:40%:20% respectively. A second division is proposed by Collinson & Goodman (1982) to include, primarily grazers (90 - 100%) feeding on medium to tall grass of moderate quality (bulk grazers), primarily grazers (90 - 100%) feeding on short grass of high quality (concentrate grazers), mixed feeders (11 - 89%), and primarily browsers (90 - 100%). Collinson & Goodman (1982) recommended a ratio of 45%:20%:20%:15% for classes 1 to 4 respectively.

The **feeding class** method (Collinson & Goodman 1982), where each species is allocated to a specific class, is preferred as a first estimate to the **feeding ratios** as outlined by Mentis & Duke (1976), where a portion (arbitrary) of mixed feeders is allocated to the grazer class and a portion to the browser class.

The feeding ratio and feeding class methods do not take into account different sized herbivores. A method, which considers animal impact, and which may serve as an adjunct to the latter methods is proposed by Collinson & Goodman (1982) who divide herbivores into four **feeding types.** Type I feeders have the ability to bring about drastic changes in unutilized climax vegetation. Type II feeders require relatively open areas with nearby thicker areas for shelter, do not cause substantial change to vegetation composition and structure, and decrease due to changes brought about by Type I feeders. Type III feeders increase in response to Type I utilisation and have the ability to push the vegetation state induced by Type I feeders past a threshold point which would have resulted had Type III feeders been absent. Type IV feeders may increase due to changes brought about by Type I and III species, but have little impact on the vegetation (Collinson & Goodman 1982).

Managing for heterogeneity

In heterogenous systems, particularly those which are smaller in extent and which are man-dominated, and which experience variable environmental and resource conditions, setting animal numbers is possibly the most important decision the manager has to take. Carrying capacity on the other hand is something which a manager can only aim at maintaining or improving. It is therefore important to discuss the terminology surrounding 'stocking rate' and 'carrying capacity' issues as currently used in southern Africa, while bearing in mind how these expressions relate to equilibrium/disequilibrium theory, scale and heterogeneity.

Units of expression of 'stocking rate' and 'carrying capacity'

Three approaches are presented, the agricultural approach (ha LSU^{-1}), the grazer unit ($GU\ ha^{-1}$)/browser unit ($BU\ ha^{-1}$) approach (Peel *et al.* 1991) and the biomass approach of Coe *et al.* (1976).

The Agricultural approach

The National Grazing Strategy (Anonymous 1985) specifies that grazing capacity is expressed as **hectares per large stock unit (ha LSU^{-1}).** The method uses the animal's metabolisable energy requirements and probable food intake, and comparisons are generated and expressed as LSU's (Meissner 1982). The LSU replacement values are calculated using metabolic mass ($w^{0.75}$) and a reference norm of 450 kg.

Shortcomings of this approach include:

(1) the term ha LSU^{-1} decreases in magnitude with increasing livestock numbers (Danckwerts & Stuart-Hill undated). This is misleading and is contrary to the SI units system of nomenclature (Savage 1979; Taylor 1991). As stocking rate is an expression of the number of animals per unit area, the units must reflect this, i.e. $LSU\ ha^{-1}$. In fact, as the word 'rate' is used, a time dimension is presupposed so that $LSU\ ha^{-1}$ are the units for stocking density and $LSU\ ha^{-1}\ a^{-1}$ are the correct units for stocking rate (*sensu* Trollope *et al.* 1990)(from here we use stocking density as the term describing the number of animals per unit area);

(2) the term ha LSU^{-1} is not linearly related to the number of animal units on an area of

land (Danckwerts & Stuart-Hill undated);

(3) the **LSU** is based on a heavy bodied grazing ruminant (originally a 1 000 lb ox!) and does not take into account the feeding patterns (overlap) and digestive systems of different herbivores. The conversion of different herbivores, particularly browsers, to LSU's is therefore flawed. Even within the grazer component, the assumption that animals consume the same amount of dry matter relative to their mass, as assumed by the metabolic mass conversion, is problematic. In multi-herbivore systems this leads to confusion when calculating carrying capacity and stocking rates in terms of the currently used grazing capacity map. Dekker (1997) proposes the use of ungulate resource overlap to set up an index for incorporation into substitution ratios for calculating stocking rates. The concept is useful in that it relates the animal component (spatial distribution and habitat selection) to important habitat attributes (diet composition and browsing height) in particular;

(4) the agricultural grazing capacity map lays down a single figure, thus ignoring environmental and resource variation. This approach assumes stable, homogenous systems (Table 1 points 1 and 2); and

(5) the term grazing capacity ignores the fact that there are two forage sources, viz. grazing (provided by grass and non-woody forbs) and browse (provided by the woody component).

Shortcomings of the LSU apart, the term LSU ha^{-1} shows a linear relation with change in animal numbers and is considered more useful than the term ha LSU^{-1}.

The Grazer Unit/Browser Unit approach

To address problems such as non-recognition of different forage sources and the debatable validity of the use of the LSU, particularly for browsers, the concept of grazer units (GU - animals which graze exclusively) and browser units (BU - animals which browse exclusively) have been proposed (Peel *et al.* 1991). The equivalent GU and BU replacement values were calculated using the animals metabolic mass ($w^{0.75}$) and reference norm of 450 kg and 140 kg for the GU and BU respectively. Dekker (1997) modified Peel *et al.* (1991) by replacing the 450 kg exclusively grazing animal with a 180 kg exclusively grazing animal while retaining the browser as a 140 kg browsing animal. Animals were then allocated proportionally to GU and BU on the basis of their diet, and were expressed as Grazer Units per 100 ha

(GU 100 ha^{-1}, strictly GU km^{-2}) and Browser Units per 100 ha (BU 100 ha^{-1}, strictly BU km^{-2}). In using this method, the basic tenets of equilibrium (Table 1, points 1 and 2) still dominate. This approach however, may provide the land-user with a diversity of management options if the concepts of multi-directional succession (Table 1 point 3), Multiple Stable States (Table 1 point 4) or multi-disclimax communities (Table 1 point 5) are accepted (e.g. adaptive management to suit habitat conditions, e.g. in woodlands animal species mixes may be dominated by browser species, or the habitat may be manipulated to favour grazing species).

Shortcomings of this approach include:

(1) the inability to meaningfully determine browser stocking rates in relation to the browse resource (in dry systems the **graze** resource is generally limiting while the **browse** resource is more stable and less prone to over-exploitation (Scholes 1986); and

(2) the need to allocate mixed feeders arbitrarily on the basis of diet. This is seen as the principal shortcoming in the work of both Peel *et al.* (1991) and Dekker (1997); and

(3) as with the LSU, the presumption that animals consume the same amount of dry matter relative to their mass (as assumed by the metabolic mass conversion).

Large herbivore biomass and mean annual rainfall

Coe *et al.* (1976) related the biomass of animals carried on game areas to long term annual rainfall on 12 natural ecosystems. The model proved satisfactory for areas receiving a mean annual rainfall of up to 700 mm on granite derived soils, and provided a satisfactory **range** of stocking densities for the Lowveld areas of the Mpumalanga and Northern Provinces, South Africa. The formula uses the mean animal mass of herbivores, and the biomasses making up the animal component are summed for the individual ranches and reserves. The result is expressed in kg km^{-2}. The formula used is as follows:

Biomass of large herbivores = $8.684(\pm 2.25)AP - 1205.9(\pm 156.6)$ where AP is mean annual precipitation. Danckwerts (1982b) applied the same logic with empirical data from domestic systems.

Shortcomings of this approach include:

(1) the broad relation between biomass and rainfall does not take into account **local temporal and spatial variations** in savanna ecosystems. For example, the herbivore

biomass/rainfall relationship is modified by geomorphology which influences soil nutrient availability and ultimately the carrying capacity of African savannas (Bell 1982; East 1984). Large herbivore biomass increases with rainfall from less than 200 mm to more than 1 000 mm in areas of medium to high soil nutrient status (rift-valley sediments and soils of volcanic origin). On soils of low nutrient status (basement situations), and on soils derived from granitic continental shields, biomass increases with rainfall up to a mean of 700 mm, and then declines as rainfall increases further (Bell 1982). The addition of a coarse soil nutrient availability factor to the model of Fritz & Duncan (1994) extends the validity of their model to ecosystems receiving 1000 mm of rainfall. The latter point is currently being examined for the Lowveld savannas of South Africa using standardised helicopter count data and taking into account broad soil patterns; and

(2) Coe *et al.*'s (1976) model was based on numbers obtained from a wide variety of count methods. Bell (1982) and Fritz & Duncan (1994) contend that the count methods provided gross undercounts for many of the areas included, and conclude that the actual biomass levels may be twice as high as those indicated by the Coe *et al.* (1976) model.

Once again, if the concepts of the multi directional succession (Table 1 point 3), Multiple Stable States (Table 1 point 4) or multi-disclimax communities (Table 1 point 5) are accepted, then this approach offers the land-user a diversity of management options (e.g. where suitable habitat exists, a rare species breeding programme may be implemented where the numbers and proportions of the rare species are maximised while the numbers and proportions of competing species are limited). As with the previous method, adaptive management may be used to exploit particular habitat conditions.

Veld management

Veld management should be aimed at achieving the objectives of the land user while facilitating the sustainable utilisation of natural resources. It is important therefore that the setting of animal numbers includes an animal and resource-based approach. There is little information available on the criteria used to set up the so-called grazing capacity maps for domestic livestock, let alone for multi-species herbivore systems. Widely varying spatial and temporal heterogeneity, closely related to the scale at which areas are managed, further complicate the setting of guidelines for veld management.

This lack of information has resulted in:

(1) the alleged widespread deterioration of natural resources, in cases where lower cover and changes in species composition are coupled with an increase in bush density and a lowering of the potential of savanna areas to achieve certain laid down objectives (see Barnes (1982) and Behnke *et al.* (1993)); and

(2) large scale drought-linked animal mortality (Walker *et al.* 1987).

Discussion and possible future directions

The term 'carrying capacity' is a nebulous one, with many definitions and is difficult to determine in heterogenous environments experiencing variable environmental and resource conditions. The use of both the agricultural approach (ha LSU^{-1}), and the grazer unit ($GU\ ha^{-1}$)/browser unit ($BU\ ha^{-1}$) approach (Peel *et al.* 1991) assume that systems tend to equilibrium (assuming stability and homogeneity). The biomass approach of Coe *et al.* (1976) has a similar basis to the latter but does provide a range stocking densities for a given long term mean annual rainfall (up to 700 mm) and on soils derived from granite (as in the Lowveld area of these studies). This allows for management to take into account resource conditions at a variety of spatial and temporal scales (although this is not actually provided in Coe *et al.*).

The value of Coe *et al.* (1976) as a precursor to a coarse-scale method of determining potential animal numbers, is illustrated in the Klaserie Private Nature Reserve (KPNR). The KPNR example also illustrates an instance of equilibrium dynamics in a closed system. Stocking densities in the KPNR, similar to the single grazing capacity figure laid down by Agriculture, resulted in a large scale herbivore population crash subsequent to the 1982-83 drought (Figure 1). The cause of the population crash was precipitated by the provision of artificial water points which allowed water dependent animals in particular to increase to artificially high numbers and to alter the habitat to suit their needs. This in turn resulted in a decline in the spatial heterogeneity of the natural resources and extensive grass mortality which was exacerbated by the drought (Walker *et al.* 1987). Note that the animal mortality in the KPNR after the 1982/83 drought dropped the actual stocking density to a point near the

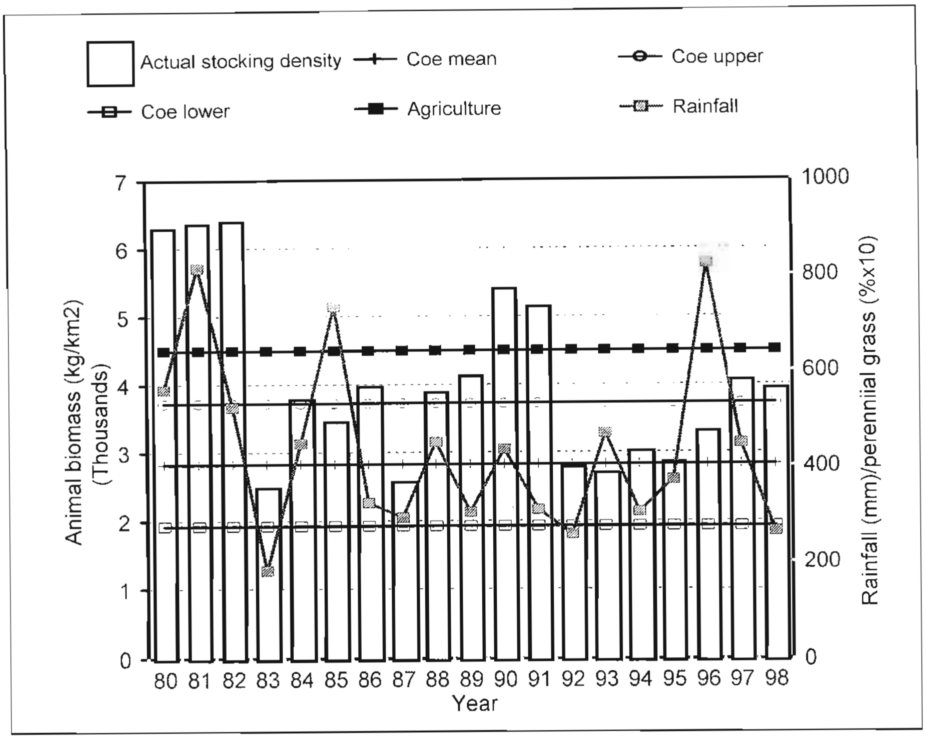

Figure 1 The fluctuation of animal density in relation to rainfall for Klaserie Private Nature Reserve (KPNR) from 1980 to 1997 (Coe- upper, mean and lower refer to the long-term stocking density estimated from Coe *et al.* (1976) and Agriculture refers to the Department of Agriculture recommendations)(data used with permission C Rowles, warden KPNR, PO Box 150, Hoedspruit, 1380).

lower guideline limit calculated from Coe *et al.* (1976). Contrasted with the above example is one from the Sabi Sand Wildtuin (SSW) (Figure 2), our interpretation of which is that rainfall may have largely dictated changes in grass dynamics with negligible stocking density implications (i.e. a 40% decline in the relative proportion of perennial grasses but with very little decline in animal biomass). The herbivore biomass method (Coe *et al.* 1976) of expressing stocking density is considered more useful than an Animal Unit-based approach as is the division of herbivores into four feeding classes (Figure 3). It is unclear which ecosystem theory in Table 1 to evoke to explain the importance of the annual grass component in supplementing the remaining perennial grasses and thus sustaining the animal biomass. In one sense, one could argue that the plant-herbivore dynamics appear superficially 'uncoupled' but almost in a converse way to that intended by Behnke *et al.*

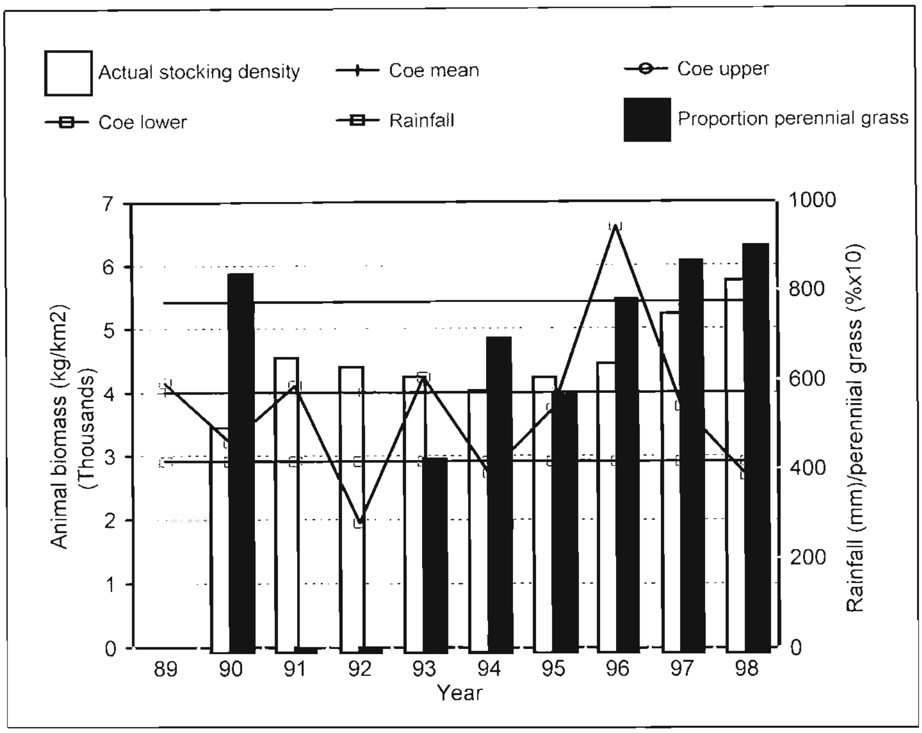

Figure 2 The fluctuation of animal density in relation to rainfall for Sabi Sand Wildtuin (SSW) from 1990 to 1998 (Coe- upper, mean and lower refer to the long-term stocking density estimated from Coe *et al.* (1976) (data used with permission B. Tavernor, warden SSW, PO Box 105, Skukuza, 1350).

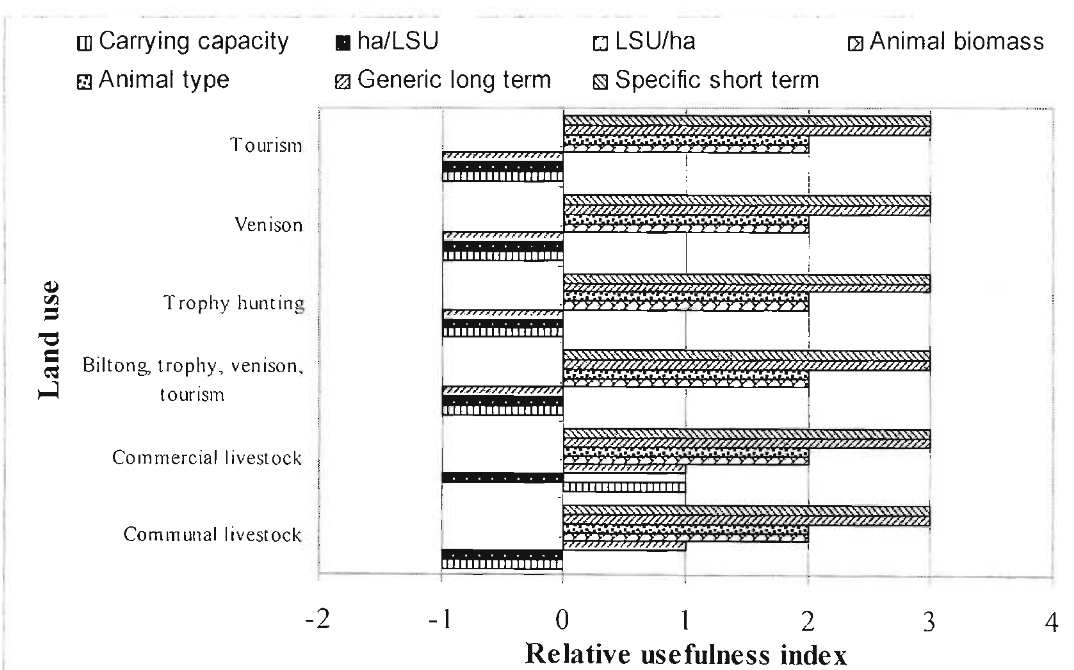

Figure 3 An evaluation of the relative usefulness (-1 = poor and 3 = good) of indices for determining (expressing) animal number and type for a range of land-use objectives in semi-arid regions of southern Africa (bottom bar in each land usecorresponds to 'carrying capacity' up to 'specific short term').

(1993)(i.e. significant changes in vegetation with no animal changes). Our prediction would be that if the particular form of the rainy season(s) following the drought had been different, and the annual crop as a result poor, then the buffering mechanism would have been far weaker, and the declines in animal biomass would have been the outcome (remembering that the re-establishing perennial component would provide little cover and forage at this stage). In another sense, this presumed buffer of annual grasses could be seen as a stochastically 'fortunate' key resource 'stabilising' an essentially equilibrial situation.

The above examples and the differing interpretations, even within examples, underline the difficulty of linking ecosystem theories to levels of rainfall, scale and heterogeneity. The level of understanding of these theories in practical situations is still limited, and may be ambivalent and at times not useful. It is likely that, in the Lowveld area of these studies, that both equilibrial and non/disequilibrial patterns are discernible at different localities and under different circumstances, or even at different time phases/scales in the same locality.

The scale at which conservation areas are managed over time and space obviously influences the 'grain' at which the 'stability-based' suite of indicators might be used. We need to understand the factors which control system functioning, which determine when, in terms of the objectives, a system is at or near a stability threshold, and how much fluctuation management is prepared to allow.

If a sufficiently small block of land can be considered homogenous enough to qualify meaningfully for a carrying capacity rating, the major remaining axis of variation in most African rangelands is varying rainfall over time. In multi-species herbivore systems, stocking densities generated at appropriate time intervals, perhaps annually under extensive circumstances, would then qualify as practicable. In the purely domestic situation on the other hand, animals could still be manipulated on a shorter temporal scale as advocated by Danckwerts (1982b). Another source of influence on these 'stability-based' recommendations is the 'entrance' condition of the range at the time the recommendation is made. It thus seems sensible that (say annually generated) range condition indicators should act as further modifiers to the initial index based on say long term rainfall.

A two-tiered decision making mechanism, based on a holistic approach to land care in multi-herbivore heterogenous systems, is advocated.

A coarse-scale approach to determining appropriate stocking densities and species mixes for a region

The animal based/long term annual rainfall approach (Coe *et. al.* 1976) and the animal/plant/long term annual rainfall based approach (Danckwerts 1982a,b) provide the basis of a coarse-scale medium to long-term 'stocking density map' for an area at a regional scale (1:250 000). The following are considered to be improvements on existing procedures:

(1) setting down a range of land-user objectives for the region (this will satisfy situations of multi-directional succession (Table 1 point 3), Multiple Stable State theory (Table 1 point 4) and multi-disclimax communities (Table 1 point 6). This will assist in avoiding the situation of resource degradation and animal loss as described by non-equilibrium theory (Table 1 point 7) and to a lesser extent disequilibrium theory (Table 1 point 8);

(2) the use of long-term annual rainfall data;

(3) the inclusion of geological data from 1:250 000 series maps (The Chief Director, Council of Geoscience, Private Bag X112, Pretoria, 0001). This addresses the broad brush approach of including soil as advocated by Bell (1982), East (1984) and Fritz & Duncan (1994);

(4) the inclusion of soils data from 1:250 000 Land Type series maps (The Institute for Soil, Climate and Water, Private Bag X79, Pretoria, 0001)(see comment for Bell (1982), East (1984) and Fritz & Duncan (1994) above);

(5) the broad classification of vegetation types for which at least woody data are available (using an appropriate classification programme, e.g. TWINSPAN (Hill 1979)). This would be further improved by superimposing a colour composite of the area for refinement of plant community mapping;

(6) use of existing medium-term (10 years) veld assessment data to provide a regional veld condition index;

(7) the determination of nutritional status of game as related to rainfall and soil patterns, stocking density, and vegetation condition (Grant *et al.* 1995);

(8) the setting of regional thresholds of potential concern (TPCs) based on 6 and 7 above; and

(9) based on points 1-8 above, setting broad annual stocking density and species mix guidelines in line with land-user objectives (keeping in mind animal performance

criteria for different sets of objectives).

A ranch-specific approach to determining appropriate stocking densities and species mixes

This step is aimed at highlighting heterogeneity and aiding in setting of stocking densities and species mixes at a finer temporal (say annual for multi-herbivore systems) and spatial scale (1:50 000). It is essentially targeted at areas where equilibrating landscapes have been anthropogenically rescaled to non-equilibrating landscapes. The following are considered useful in this approach:

(1) setting down a range of land-user objectives for the reserve or ranch (see comment regarding Table 1 under point 1 above);

(2) the use of long- and short-term rainfall data (and distribution?);

(3) the inclusion of geological data (see comment regarding Table 1 under point 3 above);

(4) the inclusion of mapped (see comment regarding Table 1 under point 4 above) and specific soil data;

(5) the classification of vegetation types (in conjunction with 6 and 7 below);

(6) the use of a remotely sensed normalised difference vegetation index (NDVI)(Tueller 1991) to provide an indication of where the active vegetation growth is occurring. This point and point 7 below addresses the issues of heterogeneity and key resource management and is also pertinent to points 8 and 10 below;

(7) the use of a moving standard deviation index (MSDI)(Tanser 1997) which identifies those areas of greatest disturbance and worst veld condition;

(8) use of short- and medium-term (10 years) veld assessment data to compare to the regional veld condition index. This will also include the evaluation of the key herbaceous variables of composition, canopy cover, height, cover, and production, and the woody parameters of composition, density, cover and structure;

(9) the determination of nutritional status of game as related to rainfall and soil patterns, stocking density, and vegetation condition (Grant *et al.* 1995);

(10) based on points 1 to 9 above, and using local knowledge and that from available vegetation data, identify the extent and condition of key resource areas. The importance of key resources depends on their susceptibility to change. If they are resistant to change then stability and resilience are conferred (Walker & Goodman

1983), and this will influence management decisions;

(11) the setting of ranch-scale thresholds of potential concern (TPCs) regarding points 2-10 above; and

(12) based on points 1-11 above, setting appropriate stocking density and species mix guidelines in line with land-user objectives (allowing for exploitation of opportunities and evasion of hazards).

These modifications to the original carrying capacity rating tend to partially satisfy in some way, the needs posed by a heterogeneity-based paradigm argued here (Figure 3). The question is whether a completely novel, yet practical approach, can be developed which is based more directly on considerations of heterogeneity. Such a product will allow us to set up a model to predict stocking density guidelines, for a range of objectives, based on a resource condition index and recent rainfall.

The coarse-scale and ranch-specific approaches as recommended here, are aimed at providing reliable guidelines for setting appropriate stocking density and species mixes for a range of land user objectives.

Tables 2 and 3 provide a subjective view of the extent to which a number of variables and theories are used in the determination of 'stocking rate', 'carrying capacity' and related indices. However, the comparisons shown in Tables 2 and 3 are sparse over large areas of the matrix, showing how few of the variables and how little of the theory are incorporated into the indices. By indicating that our coarse- and ranch-scale indices span most of these, we have little more than indicated the need for their inclusion. Much work lies ahead to operationalise these in a sensible and useful joint functionality, and to discover wider scope outside these horizons.

Table 2 Variables used in determining the indices relating to the expression of animal numbers.

Variable	Index						
	Carrying capacity	ha LSU^{-1}	LSU ha^{-1}	Animal biomass and type	Coarse-scale	Ranch- scale	Other better indices
Geology	0	0	0	1	1	1	
Soils	0	0	0	1	1	1	As yet not described
Long-term rainfall	0	0	0	1	1	1	
Short-term rainfall	0	0	0	0	0	1	
Rainfall distribution	0	0	0	0	0	0	
Vegetation classification	0	0	0	0	1	1	
Veld condition	1	1	1	1	1	1	
Thresholds of potential concern	0	0	0	0	1	1	
NDVI[1]	0	0	0	0	0	1	(Table 2 continued overleaf)

MSDI[2]	0	0	0	0	0	1
Key resources	0	0	0	0	0	1
Biodiversity (species richness)	0	0	0	0	0	0
Heterogeneity indices	0	0	0	0	0	1
Animal nutritional status	0	0	0	0	1	1
Number of variables (out of 14) incorporated in deriving index	1	1	1	4	7	12
Variables requiring examination	As yet not described					

NDVI[1] Normalised Difference Vegetation Index

MSDI[2] Moving Standard Deviation Index

Table 3 Theories used in determining the indices relating to the expression of animal numbers.

Theory	Index						
	Carrying capacity	ha LSU^{-1}	LSU ha^{-1}	Animal biomass and type	Coarse-scale	Ranch- scale	Other better indices
Equilibrium	1	1	1	1	1	1	
Stable equilibrium	1	1	1	0	0	0	As yet not described
Multiple stable states	0	0	0	1	1	1	
Multi-disclimax	0	0	0	1	1	1	
Cyclic	0	0	0	1	1	1	
Non-equilibrium	0	0	0	1	1	1	
Disequilibrium	0	0	0	1	1	1	
Scale - equilibrating landscapes	1	1	1	1	1	1	
Scale - non-equilibrating landscapes	0	0	0	1	1	1	
Theories requiring attention	As yet not described						

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Chapter 5

Environmental and management determinants of vegetation state on protected areas in the eastern Lowveld of South Africa

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Abstract

Principal driving determinants (rainfall; geology; soil; tree density and canopy cover; animal numbers and feeding classes; fire) of vegetation structure and function in the Lowveld savanna in South Africa were grouped for a seven year period to establish their influence on the limiting herbaceous layer. Grass type, abundance and cover were examined (450 sites; *c.* 4000 km^2). Using ordination, the variation and differences in the herbaceous-response variables *viz.* perennial composition and cover allowed for the broad environmental grouping of areas of similar ecological potential. We demonstrate that areas of higher ecological potential carried higher densities of large herbivores without detrimentally affecting herbaceous composition and cover. The results have implications for land users and policy makers in terms of setting animal stocking density guidelines.

Key-words: herbaceous layer, stocking density, system determinants.

Introduction

The Savanna Biome, (426,000 km^2 approximately 34%) of South Africa, is characterized by a grassy ground layer and distinct upper-layer of woody plants (Low & Rebelo, 1996). In the eastern Lowveld of this Biome, land-use practises have varied markedly over the last century, culminating in intensified multi-use exploitation of wildlife.

During the late 1800's wholesale destruction of wildlife prompted government to consider protection. In 1898, land between the Sabi and Olifants Rivers was declared a wildlife reserve, with proclamation of the Kruger National Park (KNP) in 1926

(Stevenson-Hamilton, 1929). Extensive cattle farming dominated the Lowveld west of KNP (Kloppers, undated). Land was purchased from the 1930's for game conservation and by the 1960's, private nature reserves comprising *c.* 2350 km^2 had been established. Cattle ranching continued to dominate the remaining area until the 1970's followed by a dramatic switch to wildlife. In 1992 a new era in the wildlife industry began through the removal of the fence between the KNP and these private reserves. Spatially therefore, the last century witnessed a shift from unfenced 'extensive' use of land, through fenced, smaller-scale 'intensive' use and back towards an unfenced 'extensive' situation. This had a profound effect on the structure and functioning of these savannas. To date however most research and recommendations have dealt with preservation aspects of wildlife and there is a perceived deterioration of the vegetation.

The semi-arid savannas described here are divided into moist-dystrophic and dry-eutrophic elements (Scholes, 1987), supporting a high biomass and diversity of indigenous herbivores. Savanna vegetation dynamics are primarily driven by water and nutrient availability and competition between plants for resources (Dye & Spear, 1982; Knoop & Walker, 1985; Frost *et al.,* 1986; Scholes & Walker 1993, Venter, Scholes & Eckhardt 2003). This results in neighbouring trees becoming inter- and intra-specific competitors. There is, however, a point where trees positively influence the herbaceous layer resulting in a stable herbaceous composition, cover and production because of increased litter and soil organic matter levels and improved soil moisture and nutrient levels. Conversely, while initial grass production is greatest where trees have been cleared, this is often followed by reduction in high quality productive grasses. The resulting distribution of plant quality and quantity influence the patterns of herbivory, its impact and fire behaviour. The effect of fire on trees *per se* notwithstanding, fire is probably less important than herbivory in impacting the herb layer. This is because fire generally occurs in the dry season, when grasses are physiologically less active, and high levels of herbivory often leave little fuel. In addition, manipulating herbivore numbers and the provision of artificial water points also determines vegetation dynamics especially on small and intermediate size reserves (<800 km^2 – selected as this was the the largest of the Adjacent Private Nature Reserves where animal movement is restricted by fences).

Coe, Cumming & Phillipson (1976) developed a model relating herbivore biomass to mean annual rainfall. East (1984) and Fritz & Duncan (1994) further emphasize the importance of the influence of soil moisture and nutrient status on the type and quality of the herbaceous layer, thus governing numbers and types of animals found in an area. This is demonstrated by an example from the Klaserie Private Nature Reserve where severe drought resulted in large-scale mortality among the perennial grasses, and associated large-scale die-off of herbivores (Walker *et al.*, 1987).

Scale and heterogeneity are important considerations in any natural resource-based operation. The KNP (approximately 20,000 km^2) for example adopted the Noss (1990), definition of biodiversity as an underlying basis for their revised management plan (Braack, 1997a,b). Considering biodiversity, the plan defines 'thresholds of potential concern', including a limited percentage of 'degraded' land (Peel, Biggs & Zacharias, 1998). Adjacent 'intermediate sized' reserves (approximately 200 - 900 km^2) have embraced the basic philosophies of the KNP management plan, have similar general objectives but operate at different scales (Peel *et al.*, 1998). Small fenced properties (<100 km^2) to the west, with restricted movement, have similar objectives but, because of size, present a unique set of management challenges (Peel *et al.*, 1998). In fenced areas of small/intermediate size, 'island populations' undergo more extreme eruptions in numbers with resulting vegetation over-utilisation, than in larger systems (Owen Smith, 1983).

This study aimed at furthering understanding of savanna functioning and providing sound guidelines for land users and policy makers to assist in contributing to the economic development, in harmony with social and environmental needs, of the region. Medium-term data (7 years) presented here ascertain how rainfall, soil, herbivory, fire and grass/woody ratios influence the composition and cover of the herbaceous layer which is limiting in these grazer-dominated systems. This analysis is used to propose broad guidelines for herbivore stocking density in areas of varying ecological potential and introduces the importance of controlling species mixes.

Methods

Study area and sampling

The study area (approximately 4000 km^2) is located in the eastern Lowveld (30°35' to 30°40'E; 24°00' to 25°00'S) and is dominated by ancient granitoid rocks of Swazian and Randian age, grouped together as Basement complex such as gneiss and granite (Venter, 1990). The Timbavati Gabbro (Intrusive Rocks) interrupts the Basement complex and shows at the surface as intermittent sills and dykes (Venter, 1990).

The study is situated in the Savanna Biome (Acocks (1988) and Low & Rebelo (1996)). During the study mean annual rainfall ranged from 576 mm (south), 517 mm (central area) to 463 mm (north).

We compared the medium-term effects of differing environmental and management regimes on the herbaceous layer on contiguous properties using 200 m^2 belt-transect (450 sites). The nearest plant method was used to measure herbaceous species composition and cover (based on tuft size and distance) together with the composition, density, canopy cover, and structure of the woody layer. In the herbaceous layer, both annual and perennial species were recorded accounting for bias expected from varying environmental conditions.

Based on herbaceous perennial species composition and cover, reserves were grouped together according to ecological potential scored against a 'benchmark' (highest scoring reserve). Within each group, reserves were then compared using environmental and management variables.

Animal stocking densities and species mixes were determined using annual helicopter-based game counts and expressed in kilograms per square kilometer ($kgkm^{-2}$). Actual stocking densities were then compared against Coe *et al.* (1976) and the single grazing capacity figure used by agricultural agencies (*sensu* Tainton, 1999). Herbivores were grouped into feeding classes following Collinson & Goodman (1982) as: (1) bulk grazers (90-100% grass, medium to tall, moderate quality); (2) concentrate grazers (90-100% grass, short, high quality); (3) mixed feeders (11-89% grass or browse); and (4) browsers (90-100% browse).

Analysis

Data from the herbaceous layer (response variable) were ordered into broad functional groups, with an accompanying index of cover (distance and tuft measures), using CANOCO (ter Braak, 1987-1992; ter Braak & Prentice, 1988) as were patterns of change in herbaceous composition and cover as influenced by environmental and management factors.

Using detrended canonical correspondence analysis (DCCA) geology, land type, altitude, rainfall (actual, 2-year and 3-year running means (YRM)), stocking density, feeding classes (diet-based; Peel *et al.*, 1998), property size, tree density and tree canopy cover were examined. The DCCA was used to test for colinearity and the identification of the most meaningful environmental variables. Because of unimodal distributions, canonical correspondence analysis (CCA) was used. The constrained ordination test determined whether the environmental variables (selected from DCCA) accounted for variance and to identify which response variables were most closely associated ($P<0.05$) with individual environmental factors, these being examined using the Monte Carlo permutation tests of the first two axes. Forward step-wise multiple regression determined which environmental variables ($P<0.05$) would be included in the model. The CCA was repeated using non-management variables as covariates.

The CCA yielded a grouping of reserves whose response variables reacted similarly to the driving variables. To determine whether the reserve groupings obtained using the CCA were meaningful; a single factor ANOVA was conducted using herbaceous perennials as response variables. Similarly ANCOVA was used for the CCA with geology, land-type and rainfall (2-YRM) as covariates.

Within the groupings obtained above, important environmental and management variables were compared, for each reserve, to a 'benchmark' for that group based on herbaceous composition and cover. This analysis was used to present a guideline stocking density by comparing areas of similar ecological potential but with differing veld condition trends and stocking density. Stocking density was compared to calculations from Coe *et al.*, (1976) and the 'agricultural' value (*sensu* Tainton, 1999).

Linear trend lines were applied to veld condition and related to stocking density.

Results

Accounting for colinearity, the following environmental variables were selected for inclusion in the final ordination; geology, land type, rainfall (2-YRM), stocking density, feeding classes 2, 3 and 4, tree density and tree canopy cover. Using all of the data in a CCA, rainfall (2-YRM), stocking density, feeding classes, geology and land type contributed to explaining the variance ($P<0.05$; Fig. 1), with the first four axes explaining 99.0% and 17.1% of the species/environment and the response variables ($P<0.05$) respectively. The importance of rainfall (2- YRM), stocking density and fire as related to perennial grass proportions and tuft size, and the other important perennial grass cover variable, distance, is strongly influenced by geology and soils (Fig. 1). The distribution of sites with similar 'ordination shapes' was used to group reserves whose response variables reacted similarly to the principal driving variables. Group A represents Higher Potential Higher Stocking density (HPHSR), B Higher Potential Lower Stocking density (HPLSR), C Lower Potential Higher Stocking density (LPHSR), and D Lower Potential Lower Stocking density (LPLSR). Each group was then compared to the other groups using ANOVA.

The results indicate a difference ($P<0.05$) between the perennial grass component across groups. These differences (Fig. 2) indicate the range of values within a group which is useful in determining upper and lower guidelines relating to management decisions, such as stocking density and these upper and lower limits are related to healthy and degraded resource conditions respectively.

The CCA was repeated using the non-management environmental variables as covariates. The first four axes explained 99.5% ($P<0.05$) of the variance in the species-environmental correlation. A smaller percentage of the variation in response variable data is explained indicating that management practices such as stocking density, feeding class proportions, and fire play an important role in the dynamics of these semi-arid systems (Fig. 3). Again the distribution of sites in ordination space was used to group reserves where vegetation responded similarly to important management variables.

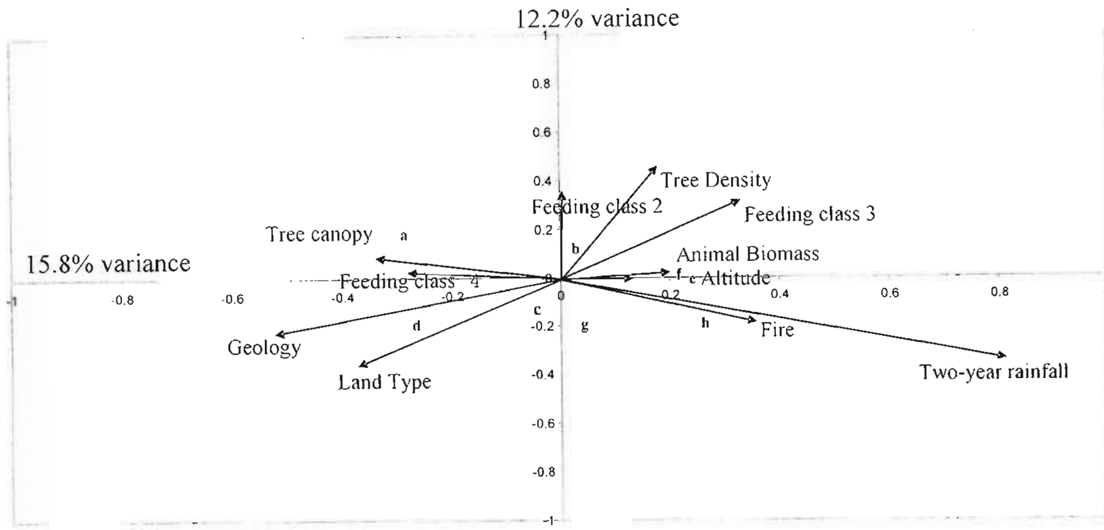


Fig 1 Biplot of CCA output showing the major environmental variables of the system and characteristics of the herbaceous layer. Where a, annuals; b, distance to all grass plants; c, distance to annuals; d, distance to perennials; e, perennial grasses; f, tuft sizes all grasses; g, tuft size annual grasses; h, tuft size perennials.

Group A represents HPHLSR, C LPHSR, and D LPLSR. Each group was again compared to the other groups using ANCOVA demonstrating differences ($P<0.05$) in the response variables between the groups (Fig. 4). This is useful in examining the upper and lower limits relating to management actions. Two reserves were compared in the higher potential group (group A; Fig. 4) and two in the lower potential group (groups C and D) in terms of veld condition trends and important driving (including management) variables.

For group A (Fig. 5, top) the rainfall for the study was not different ($P>0.05$) for the selected reserves. While the veld condition improved on both reserves, the positive slope for reserve 1 (Fig. 5 bottom) was steeper ($P<0.05$) than reserve 6 (Fig. 5 middle). Note, however, that the stocking density on reserve 6 during the study (8626 kgkm^{-2} to 14,357 kgkm^{-2}) exceeded the agricultural guideline, the upper guideline from Coe *et al.* (1976) and that of reserve 1 (4400 kgkm^{-2} to 5752 kgkm^{-2}). The stocking density on reserve 1 increased to a point marginally above the upper Coe *et al.* (1976) and the agricultural guideline. The proportion of selective grazers was low for both reserves,

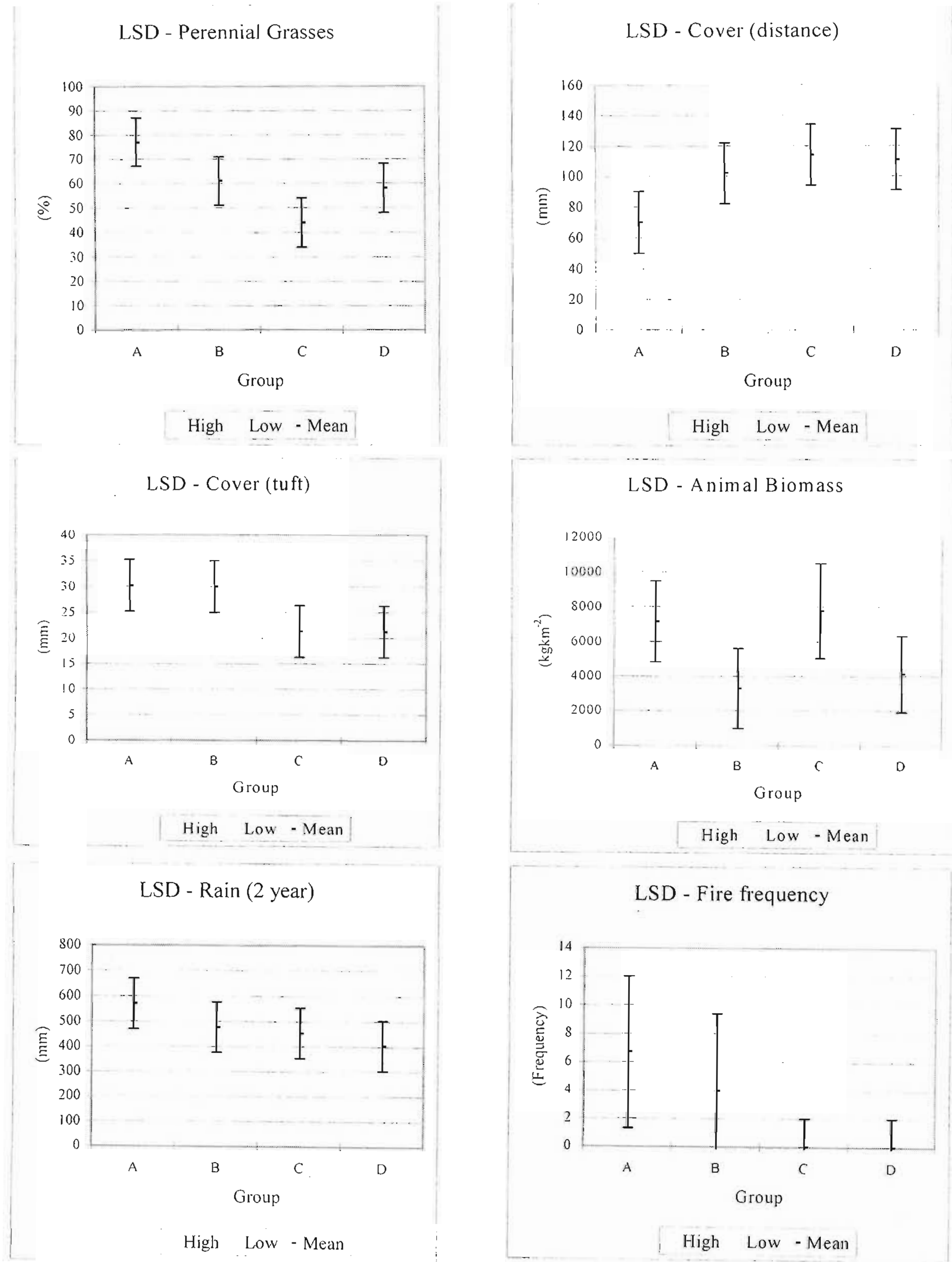


Fig 2 Differences per group and between reserves within a group.

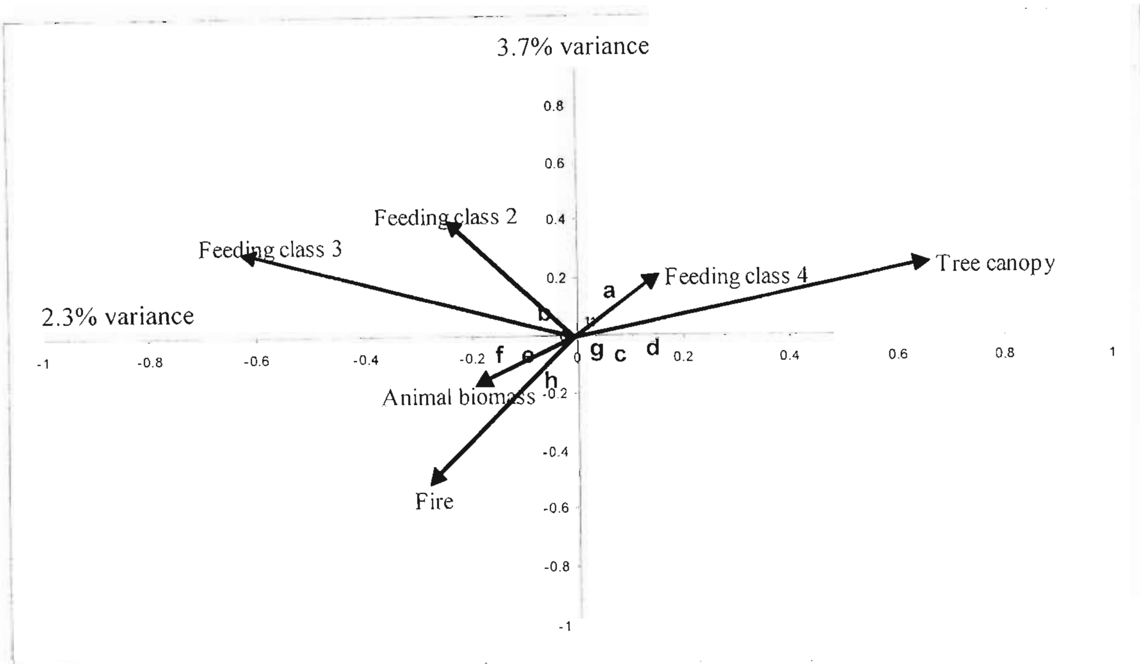


Fig. 3 Biplot of CCA showing the importance of the major management environmental variables of the system. Where a=annuals, b=distance to all grass plants, c=distance to annuals, d=distance to perennials, e=perennial grasses, f=tuft size all grasses, g=tuft size annual grasses, h=tuft size perennials.

reserve 6 (12.1% - 17.4%) and reserve 1 (1.9% - 6.1%). Because of an influx of elephant, the proportion of mixed feeders was considerably higher on reserve 1 (34.8% - 58.8%) than reserve 6 (5.6% - 21.5%).

For reserve groups C and D, one reserve from the LPHSR and one from the LPLSR were compared. The rainfall for the study period was not significantly different (P>0.05) for the selected reserves (Fig. 6, top), however, the veld condition trend was (P<0.05), with a steep decline on reserve 10 (Fig. 6 middle) and a slight improvement on reserve 24 (Fig. 6 bottom). The stocking density on reserve 10 (8353 kgkm^{-2} – 12,285 kgkm^{-2}) was much higher than the agricultural guideline, the upper guideline of Coe *et al.* (1976) and that of reserve 24 (2680 kgkm^{-2} - 5624 kgkm^{-2}) which was close to the upper Coe *et al.* (1976) and agricultural guideline. The proportion of selective grazers was considerably different on both reserves, reserve 10 (5.4 % - 22.0 %) and reserve 24 (14.6 % - 31.0 %). The same pattern of variation was observed in the proportions of mixed feeders on reserve 10 (3.0 % - 25.0 %) and reserve 24 (10.4 % - 32.0 %).

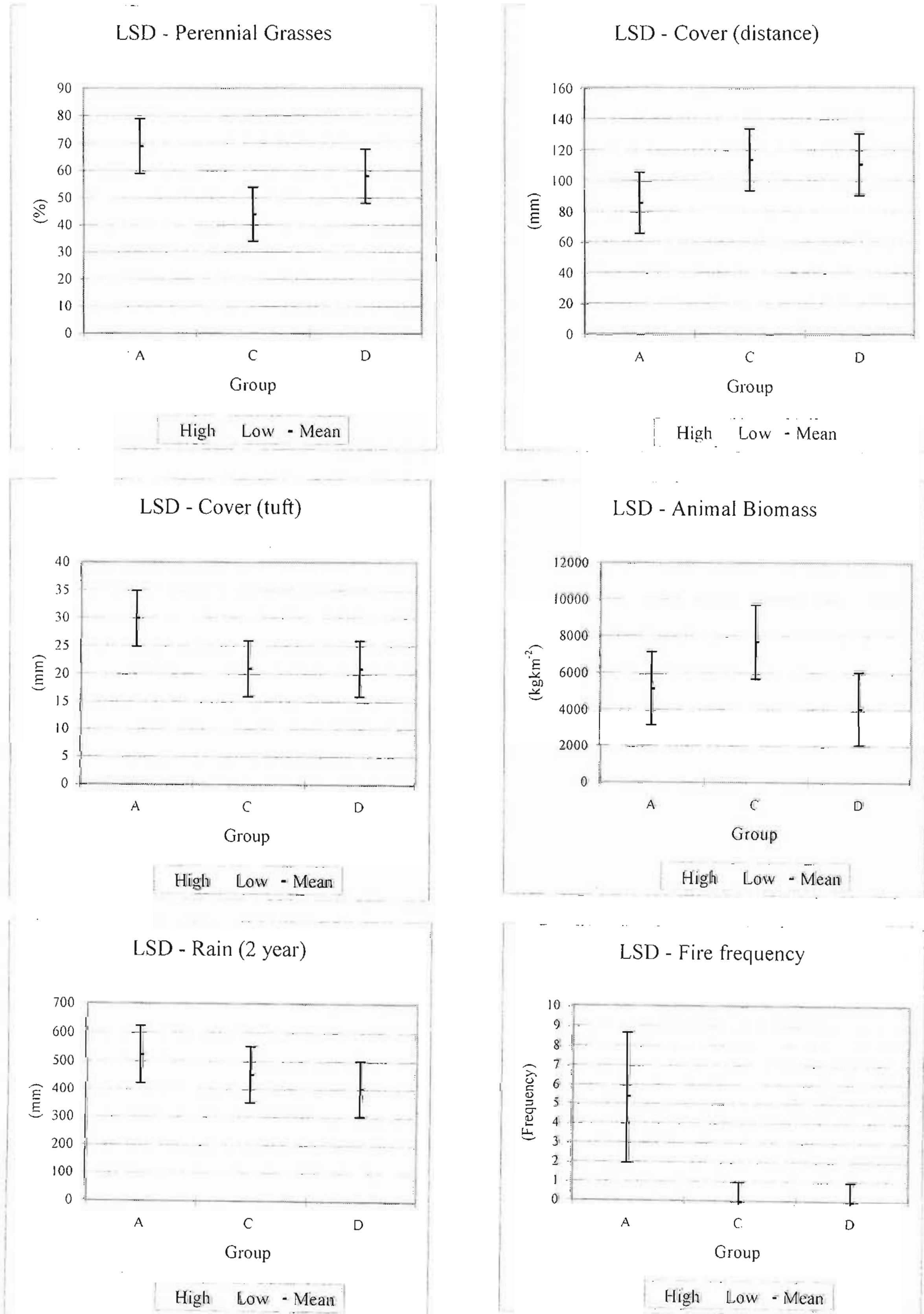


Fig 4 Differences per group and between reserves within a group.

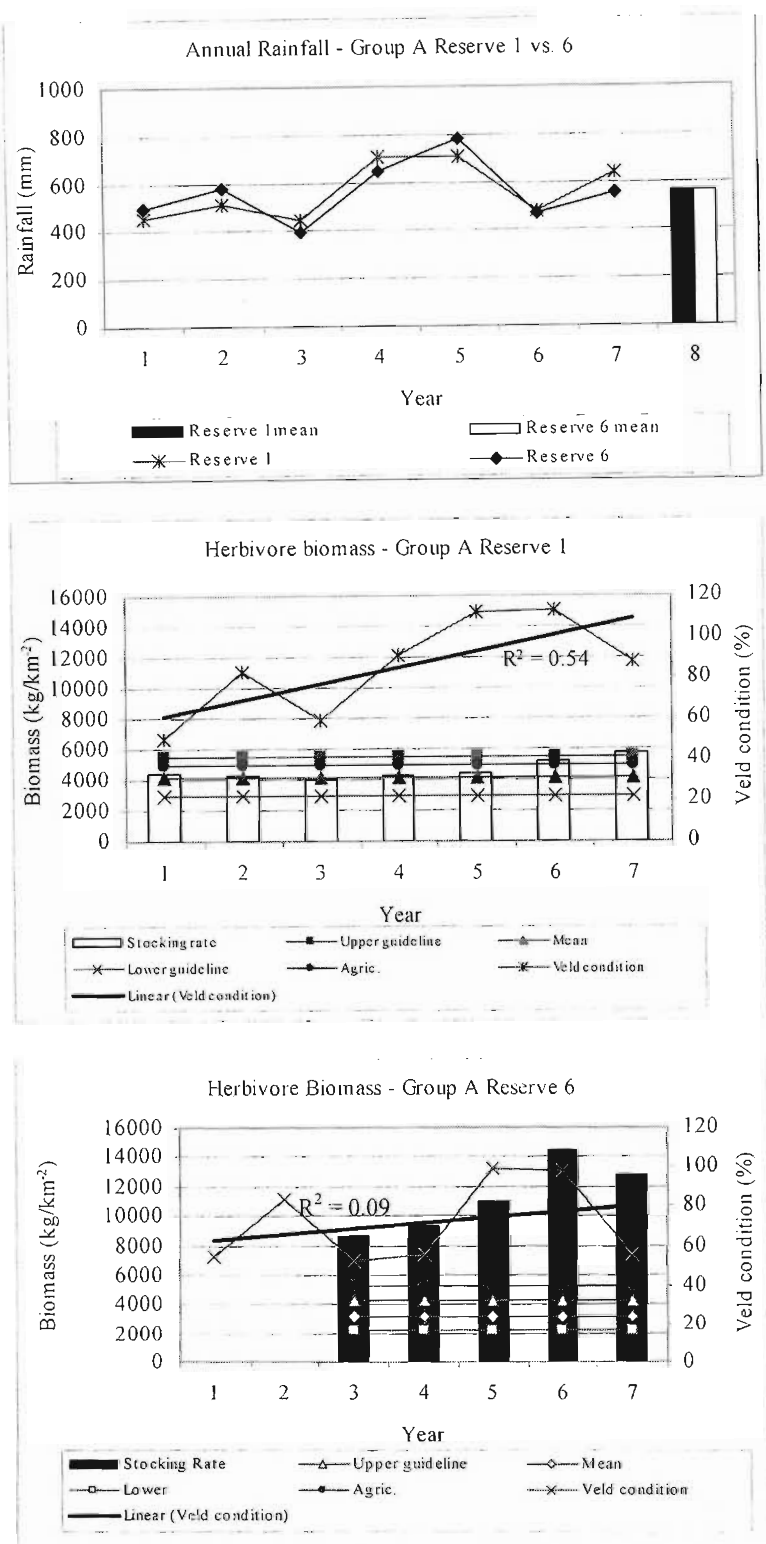
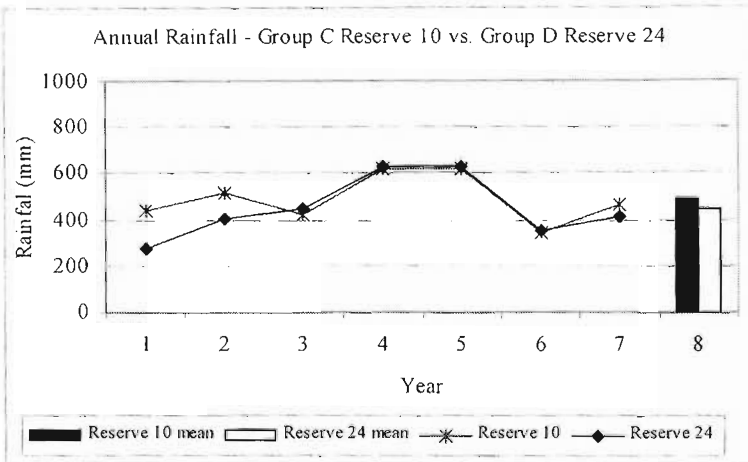
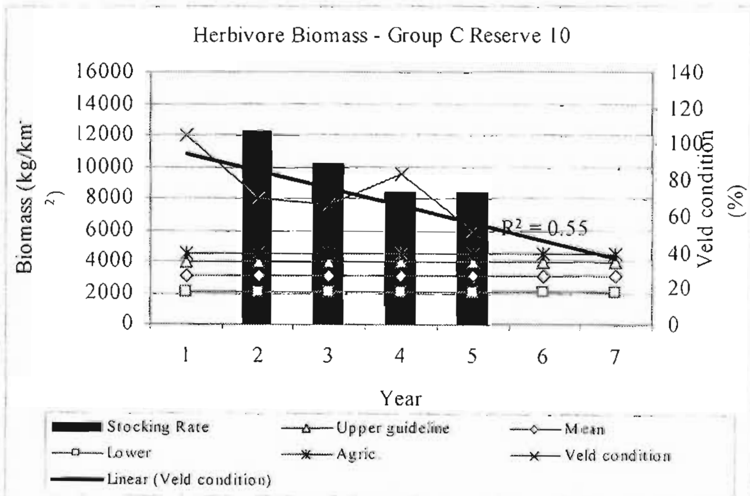


Fig 5 Group A – top: rainfall reserve 1 versus reserve 6; middle: herbivore biomass reserve 1; bottom: herbivore biomass reserve 6.





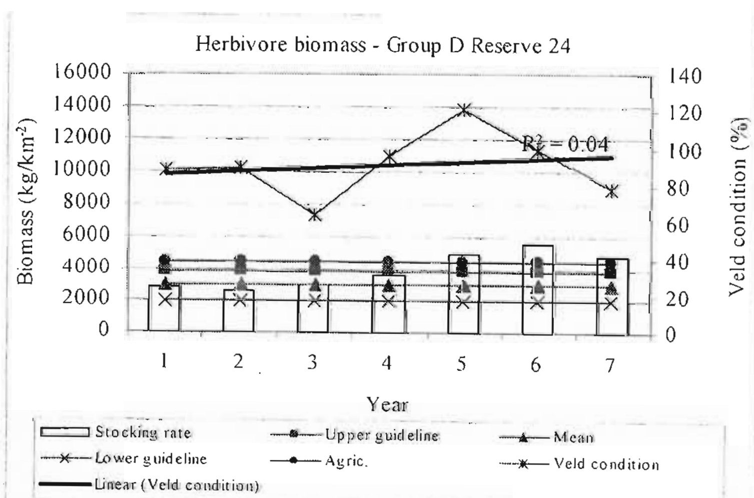


Fig 6 Group C/D – top: rainfall reserve 10 versus 24; middle: herbivore biomass reserve 10; bottom: herbivore biomass reserve 24

Discussion

The CCA indicates a higher proportion (P<0.05) and better cover (P<0.05) of perennial grasses in the HPHSR group (A) than in the rest of the study area. In terms of the major environmental driving variables that were identified, this is ascribed to deeper more fertile soils and higher rainfall, and subsequently better plant available moisture and nutrient availability than the other areas. This group therefore has a higher potential reflected in substantially elevated stocking densities than the rest of the study area (Fig. 2). The importance of physical environment is confirmed by the fact that the ranches in the LPLSR group (D), with less rainfall (P<0.05) and poorer soils (P<0.05), and more lightly stocked (P<0.05), have poorer perennial composition (P<0.05) and cover (P<0.05) (Fig. 2). Similarly for the LPHSR group (C) which is more heavily stocked (P<0.05) (Fig. 2). The above illustrates that the reserves in the LPHSR and LPLSR groups have inherently lower carrying capacity than those in the HPHSR and HPLSR groups.

Because of higher rainfall and greater fuel loads, the frequency of fire in the reserves in the HPHSR and HPLSR, and subsequent HPHLSR, is higher (P<0.05) than for the rest of the study area (Figs. 2 and 4). This indicates that fire, when used opportunistically in the higher potential areas, appears to have a positive effect on perennial composition and cover. Fire generally occurs in the dry season (May to October) and may speed up nutrient cycling by reducing plant litter and dead wood. Whereas most adult woody plants are fire-tolerant, fire does limit the establishment of woody plants, retards the development of a closed canopy and facilitates the coexistence of trees and grasses by altering the physiognomy of woody plants. This in turn promotes further fires, allowing for the maintenance of grass and fire in the system. The provision of artificial water in seasonally waterless areas, particularly in lower potential reserves (LPHSR and LPLSR), results in an eruption of water-dependent herbivores which considerably reduces fuel loads and diminishes the use of fire.

Tree canopy cover for the HPHLSR group is lower (P<0.05) than the mean for the study area. High tree densities and lower canopy cover suggests that larger trees provide most of the canopy, with smaller less established trees, where most seasonal fluctuations in density occur, contributing less to canopy cover. This is important when deciding on bush thinning strategies.

When the environmental variables were used as covariates three discrete groups were identified. All representatives of the HPLSR group B with their lighter stocking density were located in ordination space with the HPHSR group A (forming the HPHLSR group A) and the herbaceous perennial composition and cover remained higher ($P<0.05$) than the rest of the study area (Fig. 4). While the HPHSR group of the first CCA provides an acceptable (upper) guideline stocking density for the higher potential areas, the second CCA provides an acceptable guideline for a larger area, but in some instances, lower potential area. The second CCA also illustrates that the LPHSR group C is overstocked compared with the potential of the area and that a more realistic stocking density would be closer to, and probably less than, that of the LPLSR D (Fig. 4).

The positive veld condition trend on reserve 1 of group A allows for a first approximation of appropriate stocking densities for this group. By deduction, this is placed between the agricultural guideline (5000 $kgkm^{-2}$) and the highest stocking density reached during the study (5752 $kgkm^{-2}$) and similar to Coe *et al.* (1976) upper guideline (5424 $kgkm^{-2}$). The veld condition trend is positive for reserve 1 (Fig. 5c), thus raising the question whether the guideline stocking density given for group A above has not been underestimated? We contend, however, that the marked decline in veld condition during the last year of the study, although driven to some extent by below average rainfall in the sixth year of the study, may indicate some fragility in the system as regards stocking potential.

The slight positive veld condition trend on reserve 24 of group C/D allows for first indicative stocking densities for this group. Given the decline in veld condition in the latter part of the study period, this is placed between the upper Coe *et al.* (1976) (3878 $kgkm^{-2}$) and the agricultural guideline (4500 $kgkm^{-2}$). The above indicates a general decline in grazing capacity from south to north of the study area.

In addition to stocking density and fire, the CCA indicates that selective grazers, mixed feeders and tree canopy cover have an important influence on herbaceous composition and cover (Fig. 3). Selective herbivory, in particular, tends to diminish desirable forage species, while those resistant to herbivory increase. Axiomatically, because of their selective feeding, high densities of these feeding classes have a marked effect on the perennial components.

Although high impact selective grazers form a small proportion of the herbivores in the study area as a whole, it must be noted that the HPHSR group has lower ($P<0.05$) proportions than the other groups. The reserves in the HPHLSR group do, however, have higher ($P<0.05$) proportions of mixed feeders than the mean. This is due largely to an influx of elephant into these areas following the removal of the western boundary fence of the KNP in 1992. We believe that the impact of this is yet to be reflected in the vegetation parameters we measure. A contributing factor may be higher densities of trees in the HPHLSR reserves that are absorbing some elephant impact thus buffering this effect on the herbaceous layer at present (Fig. 4). The effect of high stocking densities appears to override the effect of animal feeding classes on the herbaceous layer currently.

The savannas of the eastern Lowveld can be described along a equilibrium/disequilibrium continuum that has important implications for policy and management (Peel *et al.*, 1998). Overstocking leads to animal mortality related to resource degradation (i.e. equilibrium in lower potential group C/D), or mortality related to drought where resource degradation is not as severe and where recovery is relatively rapid (i.e. disequilibrium where drought causes population declines before the herbivores modify the vegetation to an unrecoverable state in the higher potential group A). In applying the above, and considering the variation in the veld condition in our 'benchmark' reserves recently, the generic single-figure stocking density guideline is replaced by a range of possible stocking densities and species mixes. These stocking densities and species mixes are adjusted according to environmental and resource conditions on an annual basis but in some circumstances, such as droughts, possibly twice within a single season.

Through the analysis the major environmental and management variables were isolated and satisfactorily explained. This allowed for the testing of hypotheses relating to savanna dynamics and the broad grouping of areas of similar ecological potential (environment), and provides information for guiding the setting of stocking densities for the reserves at a landscape scale (1:250,000). Detailed statistical analysis is planned to refine the broad guidelines presented in this paper in a spatially explicit manner.

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Chapter 6

Thresholds, Order-of –magnitude and sustainability in African savannas

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Abstract

The study interrogates proactive management within a Strategic Adaptive Management (SAM) approach using Thresholds of Potential Concern (TPCs) as end- points on savanna ecosystems. We focus on small and intermediate size properties (<800 km^2) that because of their size, present a unique set of management challenges and advance the notion of sustainability, as opposed to biodiversity, as an end goal. Case studies compare fluctuations in the population of blue wildebeest (*Connochaetes taurinus*) and illustrate how monitoring and research feed into management by examining the potential for integrating TPCs with order-of magnitude and sustainability notions. The order-of-magnitude approach was useful in highlighting population fluctuations but was not sensitive enough and gave little indication of the cause of perturbations. The sustainability approach allowed for the construction of systematic contexts describing the systems ability to provide goods and services (or not) to achieve land user objectives. Embedded in well-articulated TPCs, the approach provided strong pointers for proactive management actions aimed at returning the system to within the limits defined by the TPCs that support the periodically reviewed objectives for the management of the land unit.

Key-words: Energy; Scale; Strategic Adaptive Management; Ecological indicators

Introduction

Savanna ecosystems, which make up some 20% of the land surface area of the world and 40% of the land surface area of Africa, are second only to tropical forests in their contribution to primary production. In South Africa 35% of the land surface comprises savannas (Scholes & Walker 1993). After assessing the value and costs of wildlife and wildlife-based activities (Peel *et al.* 2004), determining the vegetation types (Peel *et al.* 2005 *submitted*) and reviewing models for setting levels of stocking (Peel *et al.* 1998), we assessed the ecological potential and current condition of an extensive savanna at landscape (1:250 000) scale. The objective was to gain a predictive understanding of vegetation dynamics and to use the knowledge thus gained to more effectively and proactively manage such systems. We have looked at critical response variables under similar environmental and woody vegetation conditions (Peel *et al.* 2005) but with different management regimes and operating at different spatial scales (Peel *et al.* 2005). This was done within the context of bio geophysical sustainability but should rather be approached at social and economic levels (Figure 1). Sustainability is an active condition with costs and benefits and requiring knowledge and resources (Allen *et al.* 2003). We examine the concept of sustainability by examining the following approaches:

1. Order-of-Magnitude (OOM) which applies to input-output systems where ecosystem levels are determined by the balance between the rate of production (input) of a service and its rate of loss (output) (from Scholes 2002); and
2. sustainability of the bio geophysical environment based on predictability that is, in turn, affirmed or denied by the organisation of said environment as influenced by man (Allen *et al.* 2003).

Technology thus provides benefits but these come at a cost because while the initial benefits derived from using the new technology outweigh the costs of finding and implementing the solution there follows a period of diminishing return until the negative outweighs the positive (Allen *et al.* 2003). Old solutions, however, often prevail well past the breakeven point resulting in environmental degradation (defined here as a limiting of the land use options or a reduction in ecosystem services). Limits of

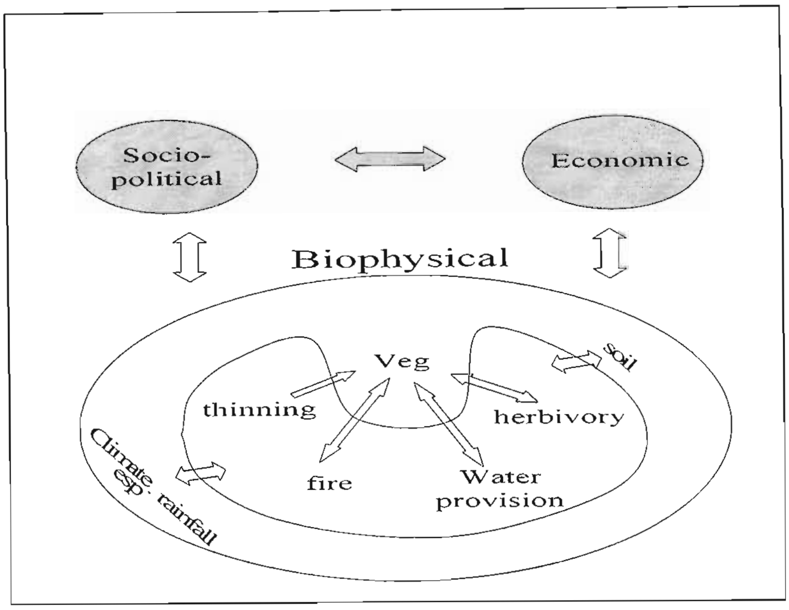

Figure 1 A schematic representation of the world we live in.

acceptable change as defined by thresholds of probable concern (TPCs) are hypotheses of spatial and temporal limits of system flux (Biggs & Rogers 2003). We integrate the results obtained above to determine the ability of the systems in question to provide ecosystem services within a TPC paradigm.

The study area

The study area (*c.* 4 000 km^2) is located within the Savanna Biome of the eastern Lowveld (Acocks (1988) and Low & Rebelo (1996)) (30°35' to 30°40'E; 24°00' to 25°00'S)). An expanded description of the area is presented in Peel *et al.* (2004).

Vision statements, land use, scale and appropriate ecological indicators

The World Conservation Strategy (WCS) provides a global approach to sustainable resource utilization (Anon., 1980; Munro & Holdgate 1991). The three main objectives of the strategy were to:

1. maintain essential ecological processes and life support systems;

2. preserve genetic diversity; and
3. ensure sustainable utilization of species and ecosystems.

In the study area, land-use practises have varied markedly over the last century, culminating in intensified multi-use exploitation of wildlife (Peel *et al.* 2004; Peel *et al.* 2005). Scale and heterogeneity are important considerations in any natural resource-based operation aimed at sustainable resource use. The KNP (*c.* 20 000 km^2) for example adopted the Noss (1990), definition of biodiversity as underlying basis for their revised management plan (Braack, 1997a; 1997b). Considering biodiversity, the plan defines 'Thresholds of Potential Concern' (TPCs), including a limited percentage of 'degraded' land (Peel *et al.* 1998). However, next to the KNP adjacent 'intermediate' sized reserves (*c.* 200 to 800 km^2) (Adjacent Private Protected Areas (APPA)) have embraced the basic philosophies of the KNP management plan, have similar general objectives but operate at different scales (Peel *et al.*, 1998). Small fenced properties (<100 km^2) to the west, which allow restricted movement for animals, have similar objectives but, because of size, present a unique set of management challenges and advance the notion of sustainability as an end goal rather than biodiversity (Peel *et al.*, 1998). In fact, there is debate as to the relation between biodiversity and stability that, depending on the degree of connectedness between species, will influence stability (May 1974). In this case Allen *et al.* (2003) relegate the notion of biodiversity to a bookkeeping exercise rather than a contribution to functional stability. Landscapes function at spatial and temporal scales that correspond with those of large ecosystems, biomes or communities (Allen *et al.* 2003). So large landscapes link easily with the processes of both smaller and larger ecosystems thus giving us an insight into ecosystems, biomes and community processes (Allen *et al.* 2003).

Until the early 1990's, most of the research work done in the eastern Lowveld dealt with the 'preservation' aspects of conservation on large reserves and national parks but there was a perceived 'degradation' of land on fenced areas to the west of KNP. These areas are thus strongly influenced by anthropogenic rescaling through water provision and a more sedentary existence adopted by water dependent animals. There was no explicit cognisance of the diversity of land uses and land user objectives, which include ecotourism, recreation, breeding of rare species, hunting, biodiversity conservation and commercial and communal livestock grazing. In addition, these systems operate at a variety of spatial and temporal scales requiring different objectives relevant to different areas at differing scales thus highlighting the need for different or tailor made management approaches to meet the particular objectives (Tables 1 and 2).

At a level higher than the objectives the vision statement should explicitly embrace spatio-temporal heterogeneity based on composition, structure and ultimately system function (Biggs & Rogers 2003). We move from these broad statements, through increasing levels of detail to technically stated ecosystem and land user goals. The objectives hierarchy therefore fills in the middle ground between high level vision statements and explicit lower-level statements required to achieve such a vision (Biggs & Rogers 2003). This is a management hierarchy.

Various methods of statistical analysis were previously used to order patterns of change in herbaceous composition and cover (measured as an index of distance to and tuft size of herbaceous plants) as influenced by environmental and management factors (Peel *et al.* 2005) in the context of an objectives hierarchy. We compare a common issue in some APPAs to illustrate how monitoring and research feed into management by examining the potential for integrating TPCs with order-of magnitude and sustainability notions.

The research-monitoring-management continuum

The importance of predicting system response to environmental and management inputs has been previously highlighted and forms the primary objective of the current study (Peel *et al.* 2005). This approach, adopted by the Kruger National Park and termed Strategic Adaptive Management (SAM) differs from conventional adaptive management in placing emphasis on the forward-looking component where management is proactive rather than reactive (Biggs & Rogers 2003). Where predictability is sought, it is imperative that management, research and monitoring are inextricably linked in a coordinated management framework. However, in the past these activities have been poorly co-ordinated with the result that management, based on long-term observation,

Table 1 A hierarchy of objectives and their relevance to spatial scale in the study area.

Objective	Relevance (scale>800km^2)	Relevance (scale<800km^2)
Maintain essential ecological processes and life support systems	High	Moderate
Preserve genetic diversity	High	Moderate
Sustainable utilisation of species and ecosystems	Moderate-Low	High
Preserve plant and animal life in our country for future generations	High	High – but replace 'preserve' with 'conserve (wise –use)'
Ensure wise utilisation of non-renewable resources	Moderate-High	Moderate-Low
Enrich qualities of life for South Africans	High	Moderate-Low

Table 2 Relations among scale, ecological theory and limits of acceptable change.

Scale	Appropriate activity/ limits of acceptable change	Ecosystem process	Indicators			Risk	
			Stability	Flux	Biodiversity		
Small – ranches	Focused	Segments	High	Maintain state	Moderate/ Low	High - less resilient	Quick shifts
Intermediate – Large reserves		Medium scale	High/ Moderate	Simulate	High/ Moderate	Moderate – but less resilient	
Large – National Parks	Wide – laissez faire	All	Moderate/ Low	Necessary	High	Low – heterogeneity buffer – spread over space – resilient – Quick (re-scaled areas) generally slow shifts	

becomes pseudo fact and many management decisions are often based on gut feeling. On the other hand, research is driven by the need to publish, which often results in useful yet highly academic contributions but difficult for managers to synthesise or apply. Quite often researchers lack the skills to translate such contributions into operational terms. Finally, monitoring generally takes place in a vacuum, providing little information for management through lack of communication while yielding few issues for in-depth research. This is because the connection between objectives of the management strategy and the gauges used to measure their attainment are not formally reviewed. We therefore adopt the approach that such research and monitoring should facilitate the effective management of the reserve to achieve the set objectives (Peel & Biggs 2002). Research should ensure that relevant, applied research projects are undertaken with the emphasis on gaining a predictive understanding of ecosystem function to serve as feedback for a SAM programme. Research should determine optimal resource levels for the achievement of land user objectives while monitoring should detect or warn of changes that conflict with the management objectives, evaluate the success of management actions, and generate relevant key questions for research and periodic revision of management objectives.

Thresholds of potential concern

The SAM approach has a strong goal-setting component and a well-developed objectives hierarchy with well-articulated monitoring endpoints (called TPCs) (Biggs & Rogers 2003). The TPCs define the spatiotemporal heterogeneity conditions for which the KNP is managed (Biggs & Rogers 2003) and are essential in connecting science, monitoring and management as embedded in an integrated ecological management programme. The TPCs are in turn defined as the upper and lower levels of ecological indictors along a continuum of change (Biggs & Rogers 2003). When a TPC is either reached or predicted to be imminent an assessment is done to decide whether management action is required or whether the TPC needs to be re-stated. The spectrum of TPCs represents an envelope within which the flux of the ecosystem is acceptable to both managers and scientists within the context of the vision statement and objectives hierarchy (Biggs & Rogers

2003). The width of the TPCs determines the level of risk that will be tolerated, e.g. widely set TPCs mean a risk tolerant approach and visa versa. For example, for blue wildebeest, the species we examine in our case studies later, the KNP set a counter trend TPC. Blue wildebeest in the KNP are particularly susceptible to predation in above average rainfall years due to increased cover for predators (Mills *et al.* 1995). The counter trend TPC is thus set for three monotonic drops of more than 10% of the estimated count in a dry cycle when in fact blue wildebeest numbers should be on the increase. Properly administered, the approach ensures that management action is correctly implemented, with the TPC, as it defines the system's current state, being returned to the acceptable range. Further, the monitoring system must be shown to be feasible and efficient with the objective being achieved by the return of the TPC to set limits (Biggs and Rogers 2003). This becomes important when considering intergenerational time scales and keeping in mind the inexorable (thermodynamic) running down of the system. If this generation for example, causes a system change it should at least be able to return the system to the current state or to a state that is capable of yielding the ecosystem services required by the next generation. The rate of change of the system also becomes important, how close are we to the edge of the cliff? Will we be able to return to the 'desired' state? We look at operationalising TPCs by investigating OOM and sustainability notions and highlight the embedding of the vision, objectives and TPCs within an adaptive management cycle and the management-research-monitoring continuum.

Order of magnitude as an approach to testing limits of acceptable change

Resilience theory suggests that ecosystems are robust within the range of variation they regularly endure (Holling 1973, Peterson *et al.* 1998). In southern African savannas, most production and loss processes for ecosystem services vary on an annual to decadal time scale by well in excess of 10% of their mean value (Scholes 2002). For example, the throughput of many processes in terrestrial ecosystems is linked ultimately to rainfall, which varies inter-annually by 20% or more on the subcontinent. Furthermore, few ecosystem processes can be measured with a high precision. There are for example large-scale fluctuations in grass yield between seasons in the study area (Peel 1996 to 2005 unpublished data). Zambatis (2003) in turn has shown inter-seasonal fluctuations of grass yield of eleven fold on the same site.

The 'Order-of-Magnitude' (OOM) technique applies to 'input/output' systems where the stock of some ecosystem service is determined by the balance between the rate of production (input) of that service and its rate of loss (output) (ICS 2002). It is a technique that is commonplace amongst engineers and physicists to eliminate unfeasible solutions (Scholes 2002).

The throughput (production or loss) (T) to the system under 'natural' circumstances is estimated to an accuracy of within one order of magnitude (Scholes 2002). The size of the net perturbation (P) resulting from the proposed action is also estimated to an accuracy of within one order of magnitude (Scholes 2002). The net perturbation is compared to the throughput (after Scholes 2002) in the following order:

1. if $P \geq T$ then the perturbation is highly likely to disrupt the supply of the ecosystem service in a meaningful way requiring either avoidance or strong mitigation; or
2. if $0.1\ T < P$ but $P < T$ (i.e. P is smaller than T, but greater than 10% of T) then it is possible that the ecosystem service will be adversely affected to an unacceptable degree; or
3. if $P < 0.1\ T$ then it is unlikely that the ecosystem service will be affected by this action alone to a degree that threatens the integrity of the future supply, or even to a degree that can be reliably measured.

Data obtained from a decade of annual total area counts indicate a marked decline in blue wildebeest numbers over large parts of the study area (Peel & Montagu 1999, Peel 2002). The relatively small size of the APPAs (see Chapters 2 through 5), makes it possible to employ annual, total area counts while maintaining suitably narrow count strips (150 m to 250 m per side depending on terrain – Bothma *et al.* 1990). The latter technique obviates the need to use the DISTANCE sampling technique which is acknowledged for areas where objects are sparsely distributed across large areas (Buckland *et al.* 1994). An OOM approach was therefore used to assess the status of two populations of blue wildebeest contained on small fenced properties (<120 km^2) within the APPAs. The results show that in extreme cases of population decline that this approach is useful, e.g. between year two and four on APPA 1 and in years 14 and 15 on APPA 2 (Table 3). Of concern, however, with this technique in these circumstances is that while the technique is sensitive when data are examined over a number of years (see years 9 to 15 on APPA in Table 3), it is not sensitive on a year-to-year basis which is generally the minimum time period over which management decisions are made. Furthermore, a result returned as P < 0.1T indicates that it is unlikely that the ecosystem service will be affected by this perturbation alone. When we look at the complete data set, however, we notice that in some cases these years mark the start of alarming declines in the blue wildebeest population (e.g. year 9 to 10 on APPA 2). The delay in management action can therefore have serious ecological and economic repercussions especially in the APPAs where prey animals are unable to move out of an area in response to predator pressure. The same principle would stand for low-density species in the KNP such as roan antelope.

The technique while useful lacks sensitivity in terms of the response to the various input versus output categories and does not meaningfully contribute to determining the cause of perturbations.

Sustainability

We acknowledge that whatever our land use objective is, we need to ensure that it is sustainable both singularly and as part of the set supporting the vision. Sustainability, however, has a generally negative connotation in that it is generally considered only achievable by using less resources and paying more for what we do consume. Allen *et al.* (2003) argue that sustainability is an active condition, not a passive consequence of doing less, and should focus on the roles of hierarchy and complexity in sustaining ecological systems and human societies. They define sustainability as maintaining or developing the systematic contexts that produce goods, services or amenities in order to achieve land user objectives at an acceptable cost for as long as they are needed or valued.

Table 3 An order-of-magnitude approach to assess two blue wildebeest populations in the APPA

Year	APPA 1				APPA 2			
	Number	Order-of-Magnitude	Colour	Action taken	Number	Order-of-Magnitude	Colour	Action taken
1								
2	251				210			
3					181	0.1T<P<T	Amber	Lions present
4	124	P>T	Red		164	0.1T<P<T	Amber	
5	102	0.1T<P<T	Amber	Lions removed	327		Neutral	Population supplemented by consolidation of property
6	138		Neutral		401		Neutral	
7	162		Neutral		484		Neutral	
8	186		Neutral	Small group of lions introduced	618		Neutral	
9	184	P<0.1T	Neutral		575	P<0.1T	Neutral	Population decimated by rapidly growing lion population
10	175	P<0.1T	Neutral	Lions removed	431	0.1T<P<T	Amber	
11	212		Neutral	Population supplemented	352	0.1T<P<T	Amber	
12	296		Neutral		329	P<0.1T	Neutral	
13	360		Neutral		298	0.1T<P<T	Amber	
14	283	P>T	Red	Population controlled – small group of lions introduced – Red ignored	123	P>T	Red	
15	305		Neutral		20	P>T	Red	

Where: 'Red' requires urgent management intervention; 'Amber' requires management consideration; and 'Neutral' requires no attention.

Scale governs the performance of a system, for example by doubling or halving the bounded size of an area we radically alter the way in which it will operate. In the study area this is central, not necessarily because the size of discrete units varies so markedly (from c. 30 km^2 to c. 20 000 km^2) but because of re-scaling of even the largest of areas through the provision of artificial water (e.g. tourism in the KNP and fencing in other areas requiring the provision of water in previously waterless areas). When looking at large systems it is difficult to know if one is fully encompassing that system. The landscape, defined in this context as 'an area with a specific geomorphology, climate, soil vegetation pattern and associated fauna' (Gertenbach 1983), can be used to detect signals at lower levels that may give us important insights into the functioning of larger ecosystems. Allen *et al.* (2003) state that populations relate downward to individual organisms and up to landscapes in that the organisms, and thus populations, are contained within a landscape in a way not possible in larger ecosystems or communities. By understanding each of the populations in the community one would not necessarily understand the issues at a community or ecosystem level hence the value of the lower level landscape scale.

Sustainability is multi-faceted, encompassing social, economic and environmental issues within a spectrum of land-user objectives. We look at sustainability as outlined by Allen *et al.* (2003):

1. manage for productive systems rather than outputs;
2. manage systems by managing their contexts;
3. identify what dysfunctional systems lack and supply that;
4. use ecological processes to subsidise management input; and
5. understand the problem of diminishing returns to solving problems.

Allen *et al.* (2003) indicate that sustainability can be achieved once we can manage the contexts of production and consumption rather than consumption itself. When the context is right the ecosystem will respond by supplying resources renewably. This, Allen *et al.* (2003) call supply-side sustainability. In the study area for example various operations are aimed at maximising economic profitability through vertical expansion of land use through consumptive and non-consumptive eco-tourism (as discussed in the following case studies). These systems are controlled one level up and management efforts are most effective when focused not on the system of interest (e.g. a species population) but on the contexts that regulate such systems (in this case the resources required by the population/s). Knowledge of the system therefore needs to be current and of a high quality and management must be focused and equipped to address the situation quickly. The former demands a co-ordinated research and monitoring effort that feeds effectively into management (see earlier discussion). Once a system decline has been corrected, not necessarily a rapid development, it is envisaged that the income generated from an increase in clients will subsidise the context within which the system functions. In this way sustainability is a topic of human values Allen *et al.* (2003) and not necessarily only an ecological condition i.e. as much an interaction between a dynamic ecosystem and a constantly changing set of human ideas (Pyne 1998). In this context therefore we look at sustainability as maintaining or facilitating the development of systemic contexts that produce ecosystem services that allow for the achievement of land-user objectives for as long as the stated objectives are considered appropriate by that generation of decision makers (after Allen *et al.* (2003). Issues around intergenerational time scales discussed under TPCs is thus relevant.

There has been some debate around 'managing for commodities vs. managing for whole systems' after the U.S. Forest Service presented empirical data to show that managing for commodities was not sustainable (in Allen *et al.* 2003). The theory has thus turned to sustainability and ultimately whole system management, including the principle of adaptive management, to sustain populations. Prediction, a central tenet of this thesis, is hard to achieve and exploratory techniques such as those presented by Peel *et al.* (2005) to propose stocking rate policies is advocated, i.e. a move from reductionism to holism based on what we understand about savanna system functioning. Using this approach, system properties are proposed and then tested using reduction to test their reliability.

Sustainability bears a cost, and cost/benefit considerations, be they ecological, economic or both, will determine whether sustainability of a certain system is in fact achievable. Allen *et al.* (2003) suggest that natural processes should subsidise the management effort, i.e. management should aim at producing outputs rather than managing for the outputs themselves. Therefore, outputs flow as a by-product of the management effort, i.e. supply-side sustainability. Before any of the above management options were tested it was necessary to ascertain whether these systems could in fact supply (resources) what the system (blue wildebeest) needs.

From Giampietro (2003), we look at an example of sustainability keeping in mind that the society, in this case blue wildebeest population, does not only depend on establishing a dynamic equilibrium between food requirements and supply. There are many other factors against which stability can be checked, e.g. are the sex ratios optimal?, is the structure of the vegetation such that predators can be detected and avoided?, is there sufficient area to move away from predators?, is there enough water in the area?, are there sufficient numbers of buffer species such as impala?, what are the densities of predators, in particular lions (*Panthera leo*), in the area?, what is the pride structure of the lions if present?

Given the validity of thermodynamics however, our first check will be to determine whether the system can indeed achieve a dynamic equilibrium where the stabilisation of the 'blue wildebeest population metabolism' requires the existence of an autocatalytic loop of useful energy (the output of energy, a stable or growing population) that stabilises the input (the number entering the system) i.e. the existence of an autocatalytic loop (which indicates a positive feedback). In order to achieve this, we use Impredicative Loop Analysis (ILA) as discussed by Giampietro (2003). Impredicativity he states, relates to the concept of the chicken and egg where the existence of a chicken is assumed so that we can get the egg to get the chicken and visa versa. Once this process is at work it is able to define itself. The process can, however, only be perceived and represented by observing at different spatial and temporal scales and we examine the vehicles of scale and criteria to address the issue of sustainability (after Giampietro 2003). The ILA therefore implies the handling of data referring to non-equivalent domains (Giampietro 2003). Data in the various quadrants of the graphs may therefore have different scales requiring a rescaling of the graphs. The graphic representations may therefore not be a regular shape to allow for the meaningful interpretation of the segments and angles. The concept of the impredicative loop should be seen as a heuristic tool that improves the scientific representation of complex systems organised in nested hierarchies. For blue wildebeest in APPA we examine the stabilisation of the endosomatic autocatalytic loop of two energy forms (after Giampietro 2003), viz. chemical energy in the food and the success of blue wildebeest expressed as survival.

Data for the model

We did two case studies of blue wildebeest populations to determine whether the individual populations were able to stabilise their own 'population metabolism' using flows of endosomatic energy (food and work) (after Giampietro 2003) and describe the loop between the different variables (Figures 2 and 3). We also examined the effect of resource use by other grazers on the blue wildebeest population by inserting the resource requirements for warthog, impala, waterbuck and zebra (Smithers 1983). The average energy demand of the different species was obtained from Meissner (1982) from which we estimate the activity patterns as they affect the feeding requirements of blue wildebeest (Berry 1982), warthog (from Cumming 1975; Mason 1982), impala (from Jarman & Jarman 1979), waterbuck (from Herbert 1970) and zebra (from Neuhaus & Ruckstuhl 2002) (Table 4). As stated by Giampietro (2003), it is possible to characterise vegetation types and wildlife systems. For example, the total size of an area is expressed in terms of different vegetation types with different production potential and different densities of associated wildlife species. We look at this approach in terms of useful energy flows into a system minus a certain fraction that is reduced by internal overheads (e.g. consumption used to maintain the population) and external overheads (e.g. predation that reduces the population). Where an indicator of environmental loading (EL), the biophysical cost of the diet, is introduced. The EL relates to the metabolisable energy of the forage (ME = 10.5 $MJkg^{-1}$ dry matter - Lombaard 1966) and the total amount of forage (from field data collection in this study). The latter takes into account the proportion of the forage that is available to the animals (estimates varying from 22% (Scholes & Walker 1993) to 49% (Grunow *et al.* 1980) in the broad-leaved savannas to between 15% (in highly nutritious systems) and 80% in fine-leaved savannas (McNaughton 1979; Drent & Prins 1987; van Wilgen & Scholes 1997; Scholes 1998).

Seasonal variation in standing crop was based on previous work done in the proximity of the study sites (Hirst 1975; Funston 1992; van Heerden 1992; Zambatis 2003). In the final case study, we look at the impact of predators on the blue wildebeest population. The direct economic implications of the two scenarios was based on the live sale 'farm gate' value of the animals in question, i.e. the income that would be derived by the reserve and not the value that the game capture outfitter would obtain from their re-sale (G. Thomson, *pers. comm.* Mohlabetsi Association of Landowners; M. Cesare, *pers. comm.* Greater Olifants River Conservancy; C. Rowles *pers. comm.* Klaserie Private Nature Reserve).

Table 4 Energy requirements and estimated activity budgets for some herbivores

Species	Energy demand MJd^{-1}	Time (%)		
		Resting and ruminating where applicable	Maintenance and reproduction	Feeding
Warthog	21.1	67	4	29
Impala	14 (graze 80%)	42	18	40
Waterbuck	34.6	38	12	50
Blue wildebeest	37.3	53	13	34
Zebra	61	33	9	58
Buffalo	101	42	8	50
Hippo	206	58	8	33
Rhino	265	37	14	49
Elephant	362 (graze 50%)	21	12	67

The model

Energy required) = $W\ (MJd^{-1})$ (from Table 4) *(1)*

Where *W* is the *energy required for the population per day 1)* is translated into an *annual energy requirement* for the population *8)* below:

Energy required) = *(1) x population size x 365d* (MJy^{-1}) *(8)*

The *total population time* available to convert food into endosomatic energy is calculated as:

Potential activity) = *24* hd^{-1} *x population size x 365d (h)* *(2)*

The largest portion of time is not related to the stabilisation of the population metabolism and so we calculate the amount of activity for *end use maintenance (M - rest) and reproduction (R)* as:

Rest overhead) = *X%* (from Table 4) *of (2) (h)* *(3)*

The *available population activity for work* (for stabilising population metabolism) is calculated as the difference between the total supply of time and the supply of time used for M&R:

Actual available activity) = *(2)-(3) (h)* *(4)*

In the population, (4) above is further reduced by *social encounters and movement* as follows:

Maintenance/reproduction overhead) = *Y%* (From Table 4*) of (2) (h)* *(5)*

The energy requirement for the population as a whole per annum is a **non-negotiable fraction** in the *supply of animal activity* of producing food. In our example, this figure is calculated as follows:

*Available activity - Food) = Z% (*Berry *et al.* 1982*) of (2) (h)* *(6)*

We now look at whether there is sufficient grass to supply the required energy to sustain the population. Where the *amount of grass required*:

Grass required) = ((8)/10.5 MJg^{-1}*)* *(7)*

With these parameters set the model can be applied.

Results and discussion

Case study 1 - Blue wildebeest population decline from 135 (y1) to 10 (y2).

This case study describes a rapidly declining population of blue wildebeest following a severe drought. We examine the energy requirements for the population singly (Figure 2a) and with potentially competing grazing species (Figure 2b).

It is apparent (Figure 2a) that although marginal, the resource is already limiting for blue wildebeest alone. We then insert the four potentially competing species using an average of time and percentage overheads for the species concerned (Figure 2b).

From this analysis we see that the resource is severely limiting when competing species are included in the model (Figure 2b). This is illustrated by mortality rates of 93%, 25%, 82% and 84% in the selective feeders blue wildebeest, waterbuck, impala and warthog respectively.

It is possible to define the density of flows for the whole system by characterising the flows for the parts. In this way we describe the decline in the wildebeest population using a variety of non-equivalent descriptive domains (after Giampietro 2003) (Figure 2c).

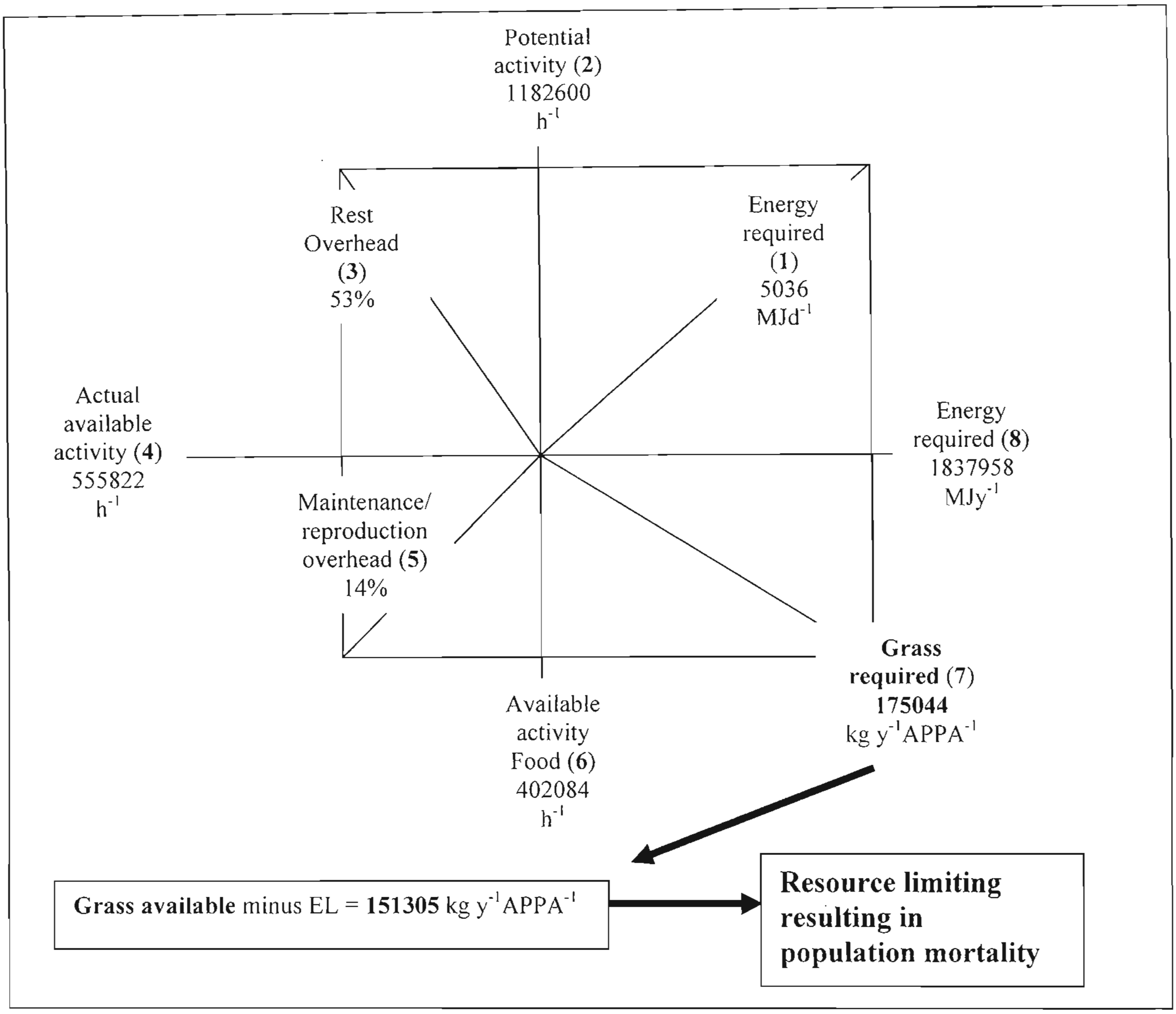

Figure 2a. A blue wildebeest population in the eastern Lowveld (north study area).

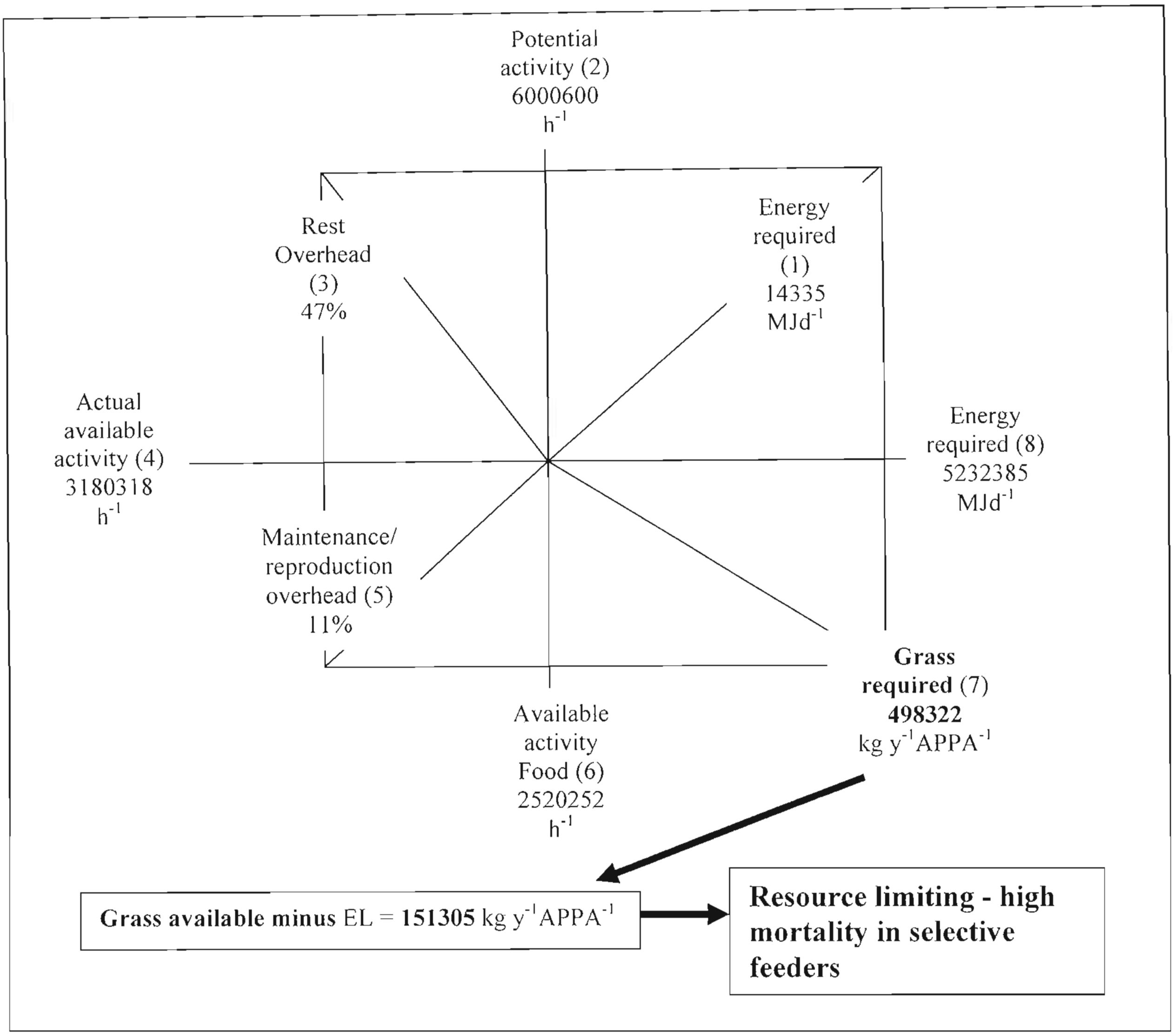

Figure 2b. Resource availability in a multi-species grazing system in the eastern Lowveld (north study area).

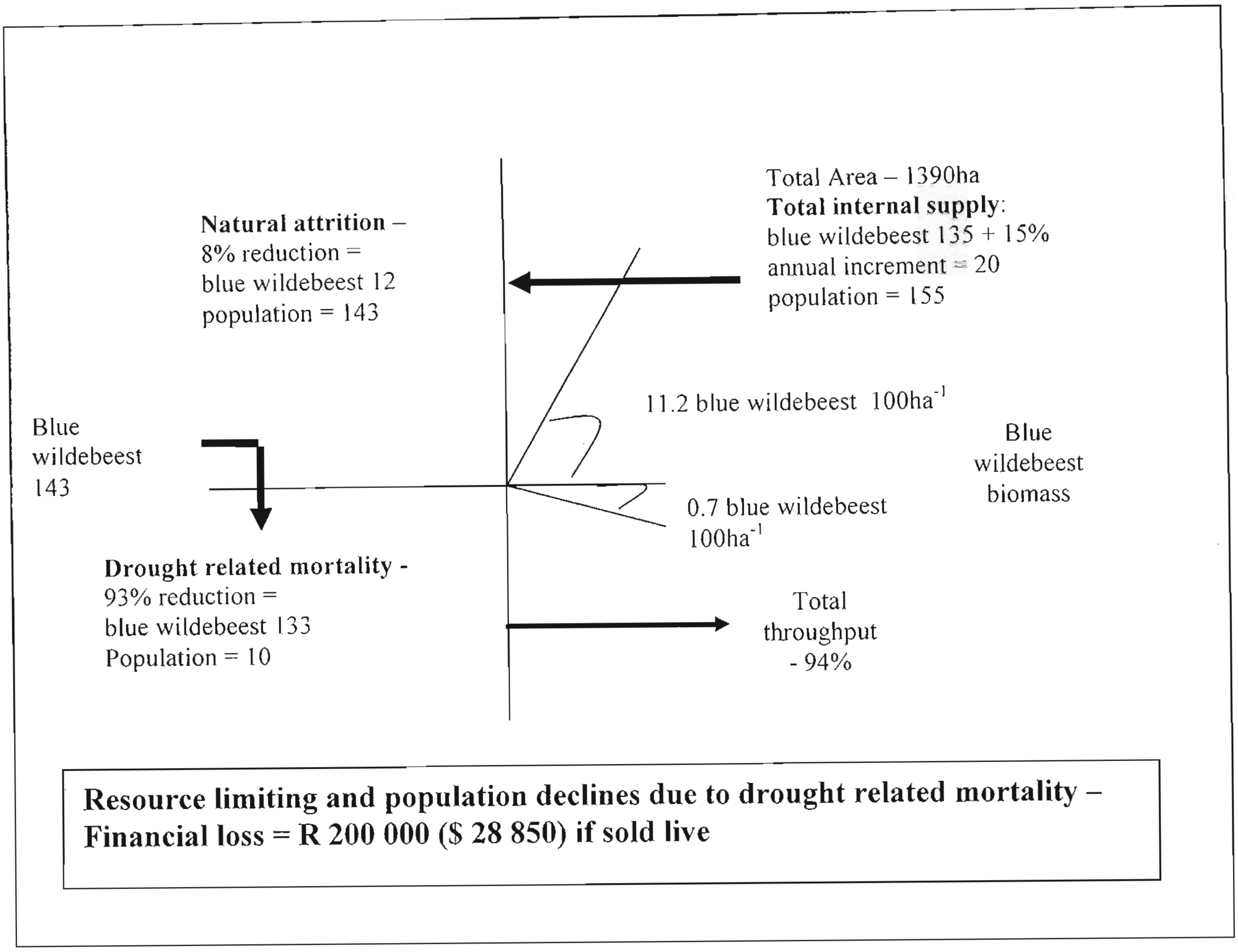

Figure 2c. Defining the density of flows for the whole in relation to the definition of the parts (after Giampietro 2003).

The land-use objective on this property is recreational tourism, i.e. largely aimed at game viewing for the benefit of the landowner and associates. Due to the multi-scaled nature of the data and using ILA, we can begin to predict population trends and implement timeous management action on a seasonal basis. Adjusting game numbers is critical on these small fenced units and decisions in this regard can be taken twice during the year, at the end of the growth season when the grass standing crop is at its highest and secondly at the end of winter following the annual game count. By looking at energy requirements and flows we can use this example to set an extreme TPC based on energy required (related to available game numbers and species mixes) vs. energy available (related to metabolisable energy and grass standing crop) on at least an annual basis.

The use of data from non-equivalent descriptive domains allows us to add economic data to the biophysical models. In the above example the loss in revenue through blue wildebeest mortality was in the region of R 200 000 ($ 29 850). As Giampietro (2003) states, making explicit such a holarchic structure using a relevant set of variables is invaluable for the study of the effect of perturbations as discussed in this example. The need for a comprehensive monitoring-research-management approach is underlined.

Case study 2 - Blue wildebeest population decline from 203 (y1) to 139 (y2)

This case study describes a blue wildebeest population that declined over a number of years. We examine the energy requirements of the population in isolation (Figure 3a) and with the same suite of potentially competing species as in the previous case study (Figure 3b). The resource is not limiting for blue wildebeest alone (Figure 3a) nor limiting after the inclusion of the suite of potentially competing herbivores (Figure 3b). There was, however, still a 32% and 11% decline in the blue wildebeest and zebra populations respectively. The waterbuck population showed a 2% decline while impala and warthog numbers increased by 2% and 12% respectively. Warthog are a species that are very susceptible to nutritional stress, and the fact that their numbers increased is a further indication that the resource base was not limiting.

Given that the blue wildebeest are the favourite prey species of lion in the study area (Pienaar 1969; Smuts 1975; Whyte 1985), and that the resource was not limiting, we included a predation factor to investigate their decline. As done previously we now define the densities of flow for the parts and in so doing describe the decline in the wildebeest population using non-equivalent descriptive domains (after Giampietro 2003) (Figure 3c).

The objective in this APPA is low volume-high paying ecotourism. The use of data from non-equivalent descriptive domains allows us to once again add economic data to the biophysical models. In the above example the loss in revenue through blue wildebeest mortality was in the region of R 200 000 ($ 29 850) if sold live. Loss of favoured prey species such as blue wildebeest ultimately results in declines in the

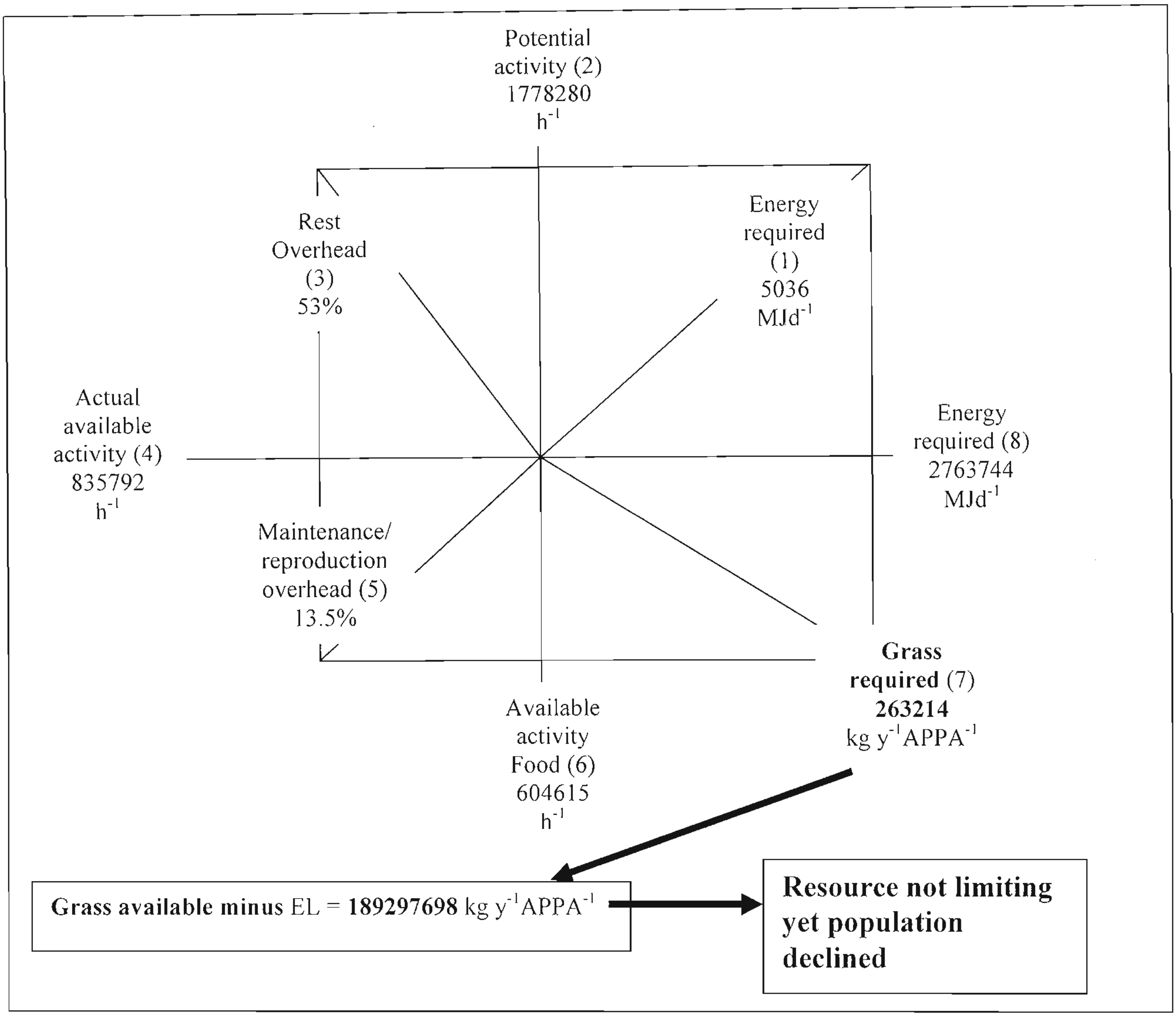

Figure 3a. A blue wildebeest population in the eastern Lowveld (south study area).

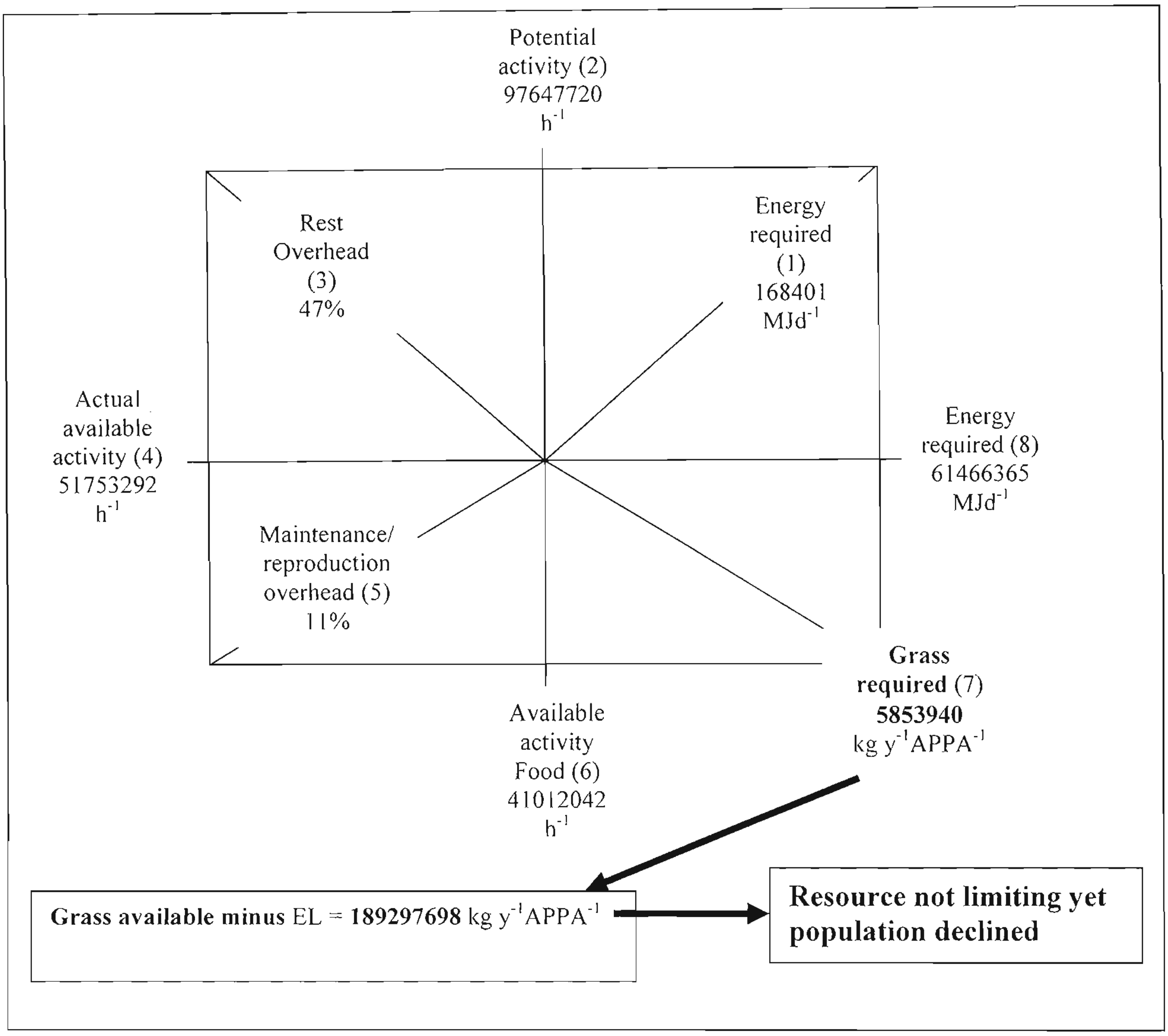

Figure 3b. Resource availability in a multi-species grazing system in the eastern Lowveld (south study area).

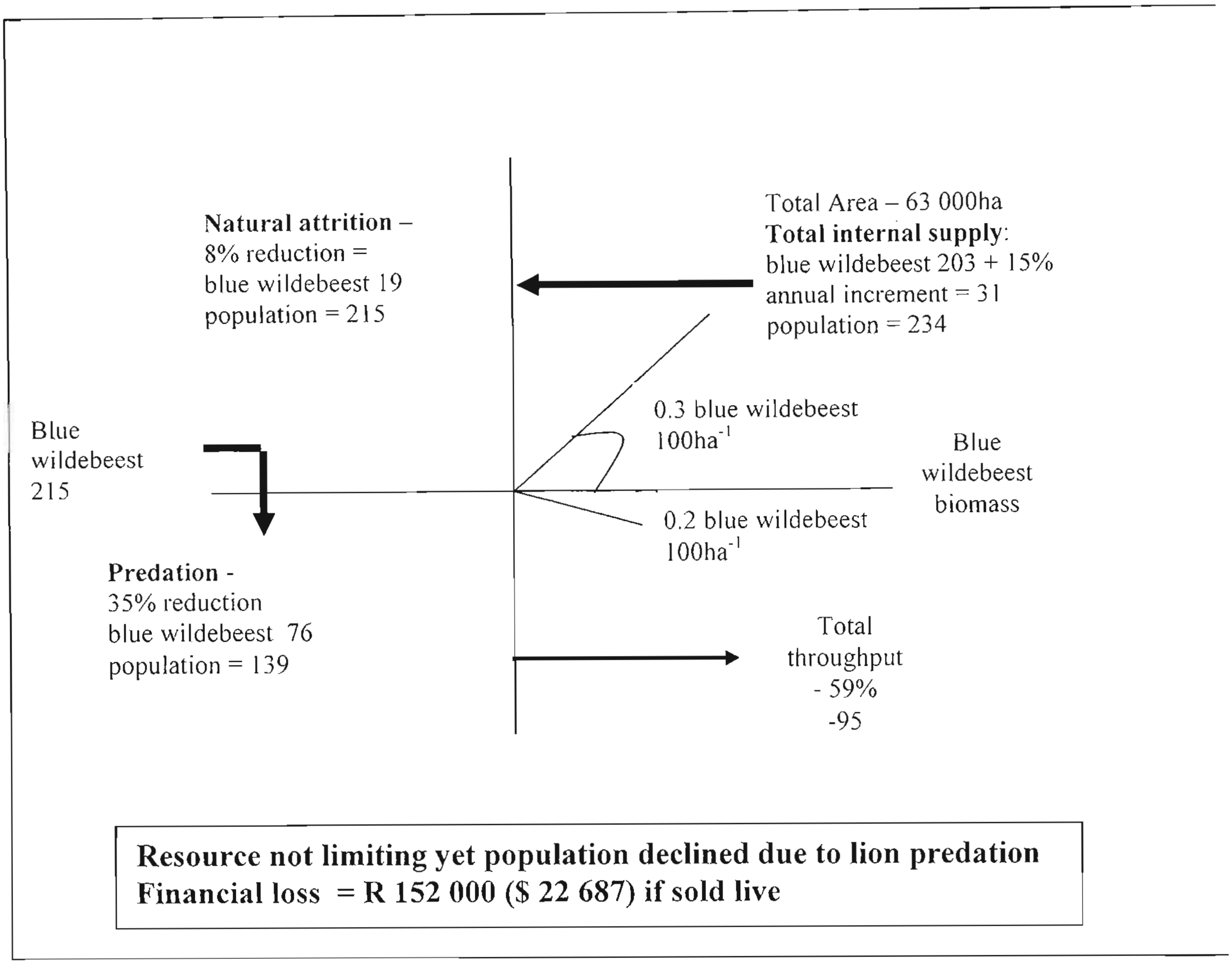

Figure 3c. Defining the density of flows for the whole in relation to the definition of the parts (after Giampietro 2003).

predator (in this case lion) populations which in turn negatively affects quality of the game viewing (another approach would be to estimate the loss of revenue if there was a decline in the number of tourists visiting the reserve).

To achieve their objectives therefore, it is necessary for operators to ensure the viewing of so-called 'Big-Five' species: lion; leopard; elephant; rhino; and buffalo. A fence erected between the KNP and the APPAs between 1959 and 1961 (Whyte 1985) to halt the spread of Foot and Mouth Disease resulted in populations of herbivores being 'trapped' in previously waterless areas. Artificial water was therefore provided resulting in the eruption of water dependent species including blue wildebeest in these areas. The increase in available prey within a confined area allowed lion numbers to increase unchecked due to an excess of available prey and no planned reduction strategy being in place. The 'trapped' blue wildebeest population began to decline and reached a point where the population was in danger of local extinction. A supply side approach to a predator/prey situation was used to address the systemic factors that allow the lions to reproduce so successfully. These systems are controlled one level up and management efforts are most effective when focused not on the system of interest (in this case the blue wildebeest population) but on the contexts that regulate such systems (in this case the resources required by blue wildebeest and the lion population).

We know that the resource is not limiting so what makes the blue wildebeest population vulnerable to excessive predation in this APPA? Woody densification has been a feature of the eastern Lowveld for at least 50 years (discussed in Peel *et al.* 2004). This places the prey species at a disadvantage due to decreased visibility of predators (Peel & Montagu 1999; Peel 2002; J. Swart *pers. comm.* Sabi Sand Wildtuin). An extensive bush thinning programme was thus put into place to 'rectify' the situation as the gently undulating landscape lends itself to limited bush thinning in the bottomlands of the catena with the more productive palatable grasses found in these areas responding well to the release from tree competition. Just above the midslope of the catena lies a band of *Terminalia sericea* that forms a Low Closed Woodland 'fringe' around the hillslope (Peel *et al. submitted*). This 'fringe' provides shelter for blue wildebeest, which feed preferentially in the open short-grass bottomlands and seek shelter in the more densely vegetated upslopes as described above. The extensive clearing of the entire slope for improved wildlife visibility for tourism in many parts of this APPA has removed this critical shelter thus allowing the lions to more easily detect their prey.

The use of ILA assisted us in formulating a suite of possible management interventions to address the situation:

1. specific restricted removal of the mobile portion of the lion population (sub-adult males) while maintaining pride integrity;
2. female lion contraception (while maintaining pride integrity);
3. re-introduction of blue wildebeest until such time as they achieve a sustainable critical population size; and
4. a halt, as far as possible, to bush clearing operations.

Addressing systemic problems in this way can be costly initially but should the programme work it would be cheaper than battling excessive outputs indefinitely. As Giampietro (2003) states, making explicit such a holarchic structure, using a relevant set of variables is invaluable for the study of the effect of perturbations as discussed in this example. As with the previous example, by taking into account energy requirements we can use this approach to set a 'safe' TPC based on energy required (related to available game numbers and species mixes) vs. energy available (related to metabolisable energy and grass standing crop). By combining the TPC values for different APPAs we may eventually have a continuum of TPCs for different areas for individual species or more significantly assemblages of species that can be related to the ecological potential of the particular area.

Conclusion

Peel *et al.* (1998) underline the difficulty of linking ecosystem theories to levels of rainfall, scale and heterogeneity. The level of understanding of these theories in practical situations is still limited, and may be ambivalent and so at times perceived as not useful. It is likely in the study area reported here that both equilibrial (a central tendency assuming stability and homogeneity) and non/disequilibrial (plant and animal dynamics are uncoupled) patterns are discernible at different localities and under different circumstances, or even at different time phases/scales in the same locality.

The scale at which APPAs are managed over time and space obviously influences the 'grain' at which 'stability-based' indicators might be used. Peel *et al.* (2005) examine the factors which control system functioning, and ultimately which determine when, in terms of the objectives, a system is at or near a threshold, and how much fluctuation management is prepared to allow it to move beyond the band of limits originally set for that threshold.

When looking at multi-species herbivore systems, Peel *et al.* (1998) proposed stocking densities generated at appropriate time intervals, perhaps annually under extensive circumstances such as those experienced in the study area, as being practicable. In the purely domestic situation on the other hand, animals could still be manipulated on a shorter temporal scale as advocated by Danckwerts (1982). Another source of influence on these 'stability-based' recommendations is the 'entrance' condition of the range at the time the recommendation is made Peel *et al.* (1998). It thus seems sensible that (say annually generated) range condition indicators should act as further modifiers to the initial index based on say long term rainfall.

While the use of variables such as long-term rainfall (Coe *et al.* 1976) and including geology (East 1984; Fritz & Duncan 1994) provides a useful platform for determining stocking densities and species mixes in savanna systems, the latter do not provide us with tools to predict savanna system behaviour and preclude the opportunity to implement proactive management interventions. Danckwerts (1982) applied the same logic with empirical data from domestic systems and went some way to presenting a predictive model that allowed for animal manipulation on a shorter temporal scale in the face of a constantly shifting mosaic of grass production. His work was carried out in a semi arid savanna in the Eastern Cape region of South Africa. The vegetation and climate are similar to that of our study save for the absence of a high proportion of broad-leaved woody species.

Peel *et al.* (1998) challenge that realistic decision-making should take place within a framework which more closely models the actual key parameters and processes in African rangelands, rather than some ideological '-ism' of near perfect or totally non-existent equilibrium. The current study thus examined sustainability embedded in a forward-looking component viz. Strategic Adaptive Management with well-articulated endpoints (TPCs). The sustainability exercise provided invaluable insight into the functioning of savanna systems by examining the outputs of the system. From the case studies we observe thus: that instead of managing for commodities within the system (e.g. a blue wildebeest population) we should manage for productive systems. This entails managing their contexts, identifying what dysfunctional systems lack and supplying that. The approach holds much promise for areas that have been anthropogenically re-scaled by the erection of fences and the provision of water for game which, in the latter instance includes substantial parts of spatially extensive areas such as the KNP. The approach elucidates why the APPAs, due to the reduced scale at which they operate, should not be managed like the KNP, but why parts of the KNP could in certain instances be managed similarly to the APPAs. This approach may in fact already provide a possible refinement to the counter trend TPC discussed for blue wildebeest earlier in the paper where a TPC is reached based merely on changes in animal numbers. Where Peel *et al.* (1998) proposed annually generated range condition indicators to determine system state, we now consider it critical to add sustainability indicators as a refinement on earlier studies. The approach and data presented in this paper, while advancement on previous efforts requires refinement in the form of better measures of available energy for individual herbivores, a developed understanding of system function to ensure sufficient energy flows and to ascertain the type and extent of energy loss via other pathways (e.g. predation). The immediate challenge is to implement this new sustainability paradigm, handling data from non-equivalent descriptive domains while providing a tool for presenting both ecological and economic variables even at differing scales. This would in turn facilitate timeous management interventions and the return to acceptable (TPC) limits based on clearly articulated objectives embedded in a comprehensive management plan. It is, of course, essential that this management plan be formally reviewed periodically. The purpose of the review would be to redefine the limits and measures of the bands that define the TPCs and other indicators of sustainability.

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Chapter 7

Summary

Savannas make up some 35% of the land surface of South Africa and in fact some 40% of the land surface of Africa. In terms of primary production, their contribution is second only to tropical forests. Further, they make up a substantial organic carbon pool that will be an important source or sink for atmospheric carbon dioxide in the future. Savannas are also home to most of the human population in Africa and form the basis of both the wildlife and cattle industries in Africa. It is therefore critical that we assess the ecological potential and current condition of extensive savanna areas at least at a landscape scale to achieve the objective of gaining a predictive understanding of savanna vegetation dynamics. The need for this study is further occasioned by the dramatic increase in land area under private conservation management and its potential to contribute to global objectives to maintaining biodiversity through sustainable management.

I outline the history of wildlife conservation and the development of the wildlife industry in the eastern Lowveld of South Africa. With the recent increases in wildlife utilization in areas to the west of the central section of the Kruger National Park (the APPAs), there arose a critical need to provide sound information for effective management. This is particularly important when we consider that most of the research work previously done was aimed at preservation strategies for large conservation areas with little information on the sustainable use of the wildlife on small and intermediate estates, many of which are fenced. In addition, woody densities have increased in many APPAs resulting in reductions within the grass layer. I examined the economic costs and ecological implications of bush control using a number of different management scenarios with differing primary objectives and based on six case studies. Encouragingly all six management scenarios examined yield positive financial returns after a ten-year projection of the modelled parameters. Ecotourism has the ability to increase the profitability of an area and as it is usually not tied to the productive capacity of the veld, it can add value beyond this through vertical expansion. Diversification of activities

through the removal of surplus game (particularly on fenced properties) increases the chances of an operation being economically and ecologically viable.

Data presented suggest that bush control (thinning) programmes, if properly planned and implemented, can be ecologically sustainable and may increase the value of land through, for example, improved game viewing for ecotourism and increased grass production. In Chapter 2, the study is thus justified on ecological and economic grounds.

Fenced areas, managed in isolation (dominated by management interventions), provided an excellent platform for empirical observations from which to deduce critical thresholds of interaction among components. This in turn presented us with insights into the relevance of ecological scaling. In Chapter 3, I look at detecting pattern and defining its spatial scale in a manner that is meaningful to management at small to intermediate scales (land areas). We know that management at local scales has a potentially critical impact at higher regional and global scales and that the direct effect of changing the degree of interaction among patches will alter system behaviour and ultimately influence higher-level processes. It is therefore critical that we assess the ecological potential and current condition of extensive savanna areas at least at a landscape scale to achieve the objective of gaining a predictive understanding of savanna vegetation dynamics. The combination of satellite imagery and objectively collected field data was satisfactorily employed to set up a classification of areas into functionally similar landscapes while allowing for up- and down-scaling. The findings of this study therefore allow us to compare critical response variables under similar environmental and woody vegetation conditions but with different management regimes. The technique thus has the potential for use in other African savannas.

Methods of determining animal densities (stocking rate) based on metabolic mass, animal type and biomass are reviewed in the context of equilibrial/disequilibrial paradigms. In South Africa, the term 'carrying capacity' is widely applied in commercial livestock systems involving one or two species. The calculation of 'carrying capacity', based on the conversion of animal species to metabolic mass equivalents assumes homogenous systems that tend to some point of equilibrium. The term is thus a nebulous one, with many assumed definitions and is difficult to determine in heterogeneous environments experiencing variable environmental and resource conditions. The use of both the agricultural approach (ha LSU^{-1}), and the grazer unit (GU ha^{-1})/browser unit (BU ha^{-1}) approach assume that systems tend to equilibrium (stability and homogeneity). The biomass approach has a similar basis to the latter but provides a range of stocking densities for a given long term mean annual rainfall (up to 700 mm) and on soils derived from granite (as in the Lowveld area of these studies). This allows management to take into account resource conditions at a variety of spatial and temporal scales. The value of the biomass method as a precursor to a coarse-scale method of determining potential animal numbers is illustrated. The herbivore biomass method of expressing stocking density in multi-herbivore systems is shown to be more useful than an Animal Unit-based approach. It is unclear which ecosystem theory to evoke to explain the importance of the annual grass component in supplementing the remaining perennial grasses and thus sustaining the animal biomass. One could argue that the plant-herbivore dynamics appear superficially 'uncoupled' but almost in a converse way to those intended, i.e. significant changes in vegetation with no animal changes. My prediction relating to an actual case study would be that if the particular form of the rainy season(s) following the drought had been different, resulting in a poor annual crop and with the re-establishing perennial component providing little forage and cover, then the buffering mechanism would have been far weaker, and there would have been declines in animal biomass. The presumed buffer of annual grasses could in fact then be seen as a stochastically 'fortunate' key resource 'stabilising' an essentially equilibrial situation.

Ecosystem theories are difficult to link to levels of rainfall, scale and heterogeneity. This demonstrates that our level of understanding of these theories in practical situations is still limited, and may be ambivalent and at times not useful. It is likely that, in the Lowveld area of South Africa where these studies were done, that both equilibrial and non/disequilibrial patterns are evident at different localities and under different circumstances, or even at different time phases/scales in the same locality.

The scale at which conservation areas are managed over time and space influences the 'grain' at which the 'stability-based' suite of indicators might be used. We need to understand the factors that control system functioning, which determine when, in terms of the objectives, a system is at or near a stability threshold, and how much fluctuation management is prepared to allow.

In multi-species herbivore systems, stocking densities generated at appropriate time intervals, perhaps annually under extensive circumstances, would then qualify as practicable. In the purely domestic situation on the other hand, animals could still be manipulated on a shorter temporal scale. Another source of influence on these 'stability-based' recommendations is the 'entrance' condition of the range at the time the recommendation is made. It thus seems sensible that range condition indicators, generated at least annually, should act as further modifiers to the initial index.

Therefore in order to effectively manage these savannas we need to understand the forces that drive them. In Chapter 5, the principle driving determinants of these savannas were grouped to establish their influence on the limiting herbaceous layer. Grass type, abundance and cover were examined to group areas of similar ecological potential. When the environmental variables were used as covariates three discrete groups were identified that reflected a general decline in grazing capacity from the south (higher ecological potential) to north (lower ecological potential) of the study area.

The savannas of the eastern Lowveld can be described along a equilibrium/disequilibrium continuum that has important implications for policy and management. Overstocking leads to animal mortality related to resource degradation (i.e. equilibrium in lower potential groups where plant and animal dynamics become uncoupled with changes in rainfall causing population declines before herbivores can influence rangelands deleteriously), or mortality related to drought where resource degradation is not as severe and where recovery is relatively rapid (i.e. disequilibrium where drought causes population declines before the herbivores modify the vegetation to an unrecoverable state in the higher potential group). The effects of fire and herbivory, while difficult to isolate, are important consumers of grass biomass in savanna systems. Archibald *et al.* (2005) showed that frequent large fires prevent areas of heavy grazing from persisting in the Hluhluwe-Umfolozi landscape of KwaZulu-Natal. The latter is a mesic savanna receiving a mean annual rainfall of around 850 mm a^{-1} (Palmer *et al. in prep.*). In contrast the current study was conducted in an area with a mean annual rainfall that ranges from 576 mm in the south to 463 mm in the north (see Chapter 5). The latter along with the re-scaling of APPAs into smaller relatively heavily stocked areas with reduced fuel loads makes fire a little used tool particularly in the drier north (see Chapter

5). In applying the equilibrium/disequilibrium paradigms outlined above therefore, and considering the variation in the veld condition in our 'benchmark' reserves recently, the generic single-figure stocking density guideline is replaced by a range of possible stocking densities and species mixes. These stocking densities and species mixes are adjusted according to environmental and resource conditions on an annual basis but in some circumstances, such as droughts, possibly twice within a single season.

Through the analysis, the major environmental and management variables were isolated and satisfactorily explained. This allowed for the testing of hypotheses relating to savanna dynamics and the broad grouping of areas of similar ecological potential (environment), thus providing information for guiding the setting of stocking densities for the reserves at a landscape scale (1:250,000). The results have implications for land users and policy makers in terms of setting guidelines for animal stocking density.

I have therefore assessed the ecological potential and current condition of an extensive savanna at landscape (1:250 000) scale, and looked at critical response variables under similar environmental (Chapter 5) and woody vegetation conditions (Chapter 3) but with different management regimes and operating at different spatial scales.

In Chapter 6, this is looked at in the context of what is considered a new paradigm for savannas in southern Africa, biogeophysical sustainability. I examine sustainability using concepts of thresholds and thermodynamics. The use of variables such as long-term rainfall and long-term rainfall with geology provide a useful platform for determining stocking densities and species mixes in savanna systems but do not provide us with tools to predict savanna system behaviour. The latter thus preclude the opportunity to implement proactive management interventions. I challenge that realistic decision-making should take place within a framework which more closely models the actual key parameters and processes in African rangelands, rather than some ideological '-ism' of near perfect or totally non-existent equilibrium (e.g. set stocking density guidelines based on long-term rainfall or inflexible species mix recommendations that do not take into account the current resource base). In Chapter 6 sustainability embedded in a forward-looking component viz. Strategic Adaptive Management with well-articulated endpoints (TPCs) is addressed. The sustainability exercise provided invaluable insight into the functioning of savanna systems by examining the outputs of the system. From the case studies, we observe thus: **that instead of managing for commodities within the system we should manage for productive systems**. This entails managing their contexts, identifying what is lacking in malfunctioning systems and supplying these. The approach holds much promise for areas that have been anthropogenically re-scaled through the erection of fences and the provision of water for game. In the case of water provision for game, this would even include substantial parts of spatially extensive areas such as the KNP. The approach reveals why the APPAs, due to the reduced scale at which they operate, should not be managed like the KNP, but why parts of the KNP could in certain instances use management strategies that are applied in the APPAs. I contend that this approach may in fact already offer a refinement to the counter trend TPC discussed for blue wildebeest in Chapter 6 where a TPC is reached based on changes in animal numbers alone. Where I proposed annually generated range condition indicators to determine system state in Chapter 4, I now consider it critical to add sustainability indicators as a refinement on earlier studies. The approach and data presented in this thesis, while an advance on previous efforts requires refinement in the form of better measures of available energy for individual herbivores, a developed understanding of system function to ensure sufficient energy flows and to ascertain the type and extent of energy loss via other pathways. The immediate challenge is to implement this new sustainability paradigm, while at the same time providing a tool for presenting both ecological and economic variables even at differing scales. By considering energy requirements we can begin to set 'safe' TPCs based on the energy needs of the animals present in an area (related to game numbers and species mixes) vs. energy available (related to metabolisable energy and grass standing crop). By combining the TPC values for different APPAs, we may eventually have a continuum of TPCs for different areas for individual species or more significantly assemblages of species that can be related to the ecological potential of the particular area. This would in turn facilitate timeous management interventions and the return to acceptable (TPC) limits based on clearly articulated objectives embedded in a comprehensive and periodically but formally reviewed management plan. **The specific purpose of which is to be proactive!**

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Appendix 1a

Title page of published work

Chapter 2 in thesis
The value of wildlife and costs of bush encroachment – Peel et al.

CHAPTER 28

The value and costs of wildlife and wildlife-based activities in the eastern Lowveld savanna, South Africa

M. Peel, R. Davies and R. Hurt

Introduction

Humans have been associated with Africa for more than two million years as hunters, pastoralists and cultivators, an association that has had a profound effect on the structure and extent of the savanna biome. Early European travellers described the sub-continent as an area inhabited by large numbers of a wide variety of wild herbivores (Grossman et al. 1999). There is, however, some conjecture as to the reliability of many of these anecdotes as early travellers were dependent on water for their livestock, which would have brought them into contact with higher concentrations of wild herbivores than elsewhere (Liversidge 1978; Grossman et al. 1999). This aside, the last half of the nineteenth century is known worldwide as the 'century of extermination' (Carruthers & Pienaar 1990). European settlers and their livestock moved into the interior of countries such as South Africa and effected large-scale reductions in the numbers of indigenous wild herbivores. The rinderpest epidemic of the 1890s further diminished herbivore numbers in South Africa. Mercifully, the 'century of extermination' was followed by the 'century of conservation' (Carruthers & Pienaar 1990). Concerted efforts during the twentieth century have resulted in an increase in the number of wild herbivores to levels where non-consumptive use is possible, and even to the point where consumptive use is necessary.

South Africa's wildlife commands a high value both regionally and globally. However, this value is often ignored because it is difficult to quantify and the depletion of wildlife and natural resources is not generally seen as an economic cost to society (Davies 1997). The value of wildlife is not fully represented in economic decisions and wildlife-based activities are often

Appendix 1b

Title page of published work

Chapter 4 in thesis

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Perspective article

The evolving use of stocking rate indices currently based on animal number and type in semi-arid heterogeneous landscapes and complex land-use systems

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Abstract

Methods of determining stocking rate based on metabolic mass, animal type and biomass are reviewed in the context of equilibrial/disequilibrial paradigms. In South Africa, the calculation of'carrying capacity' is based on conversion of animal species to metabolic mass equivalents. This assumes homogenous systems that tend to some point of equilibrium. It is applied widely in commercial livestock systems involving one or two species. Examination of a case study in the Lowveld of the Northern Province, South Africa, showed that the determination of 'stocking rate' in this multi-herbivore and heterogenous system, overestimated the 'carrying capacity' of the reserve over 20 years. The actual animal numbers in the system dropped by approximately 4 000 kg km~^{2} after a drought in the early period of the study into the bounds as determined by a model incorporating rainfall and animal biomass. An approach to determine stocking density using animal type, biomass, rainfall and vegetation parameters is suggested. The development of this as a coarse-scale (regional) and ranch-specific model to cover a range of scales and heterogeneity in key resources is advocated.

Additional index words: Animal biomass, carrying capacity, stocking density.

Introduction

In its essence the notion of 'carrying capacity', and to an extent the related indices 'grazing capacity' and 'stocking rate', presupposes a sufficiently homogenous system with a known or supposed optimal point of 'stability' based on equilibrium theory, non-deterioration of vegetation or soil over an extended term, and a land-use objective of maximising animal production (Danckwerts 1982a; Trollope *et al.* 1990). Trollope *et al.* (1990) first express 'carrying capacity' as ha AU"^{1} (Animal Unit) or AU ha"^{1}), later dividing the term into 'Grazing/Browsing Capacity' based on the fact that there are both grazeable and browseable components to the vegetation. The original 'carrying capacity' concept is advanced by the introduction of an economic element and the term 'economic carrying capacity' (Caughley 1979; Danckwerts 1982a). A related term defines 'ecological carrying capacity' (often used as a yardstick in ecotourism) as the population size of an organism in an area as determined by the capacity of that area to support the individuals in that population and enable them to reproduce (Caughley 1979; Grossman 1984).

Ecosystem functioning in African savannas has been variously described along a stable (equilibrium) - unstable (disequilibrium) continuum. 'Stable state' thinking as described above, while still obviously useful and widely applied in commercial agriculture, has been aggressively challenged by the disequilibrium school, espoused at very developed levels in Behnke *et al.* (1993). Two of the more extreme claims made by Behnke *et al.* (1993), are that there is no central tendency (point of equilibrium) operating in these systems, and that plant and animal dynamics are uncoupled (changes in rainfall causing population declines before herbivores can influence rangelands deleteriously).

This shift in thinking is attributed to the fact that arid and semi-arid African environments are heterogeneous, highly changeable and complex, rather than homogenous, Clementsian in progression and culminating in a stable climax community. Under such conditions,

Appendix 1c

Title page of published work

Chapter 5 in thesis

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Environmental and management determinants of vegetation state on protected areas in the eastern Lowveld of South Africa

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Abstract

Principal driving determinants (rainfall, geology, soil, tree density and canopy cover, animal numbers and feeding classes, and fire) of vegetation structure and function in the Lowveld savanna in South Africa were grouped for a 7-year period to establish their influence on the limiting herbaceous layer. Grass type, abundance and cover were examined (450 sites; approximately 4000 km^2). Using ordination, the variation and differences in the herbaceous-response variables viz. perennial composition and cover allowed for the broad environmental grouping of areas of similar ecological potential. We demonstrate that areas of higher ecological potential carried higher densities of large herbivores without detrimentally affecting herbaceous composition and cover. The results have implications for land users and policy makers in terms of setting animal stocking density guidelines.

Key words: herbaceous layer, stocking density, system determinants

Resume

Les principaux determinants moteurs (precipitation, geologie, sol, densite d'arbres et couverture de la voute: nombre d'animaux et classes alimentaires; incendie) de la structure et fonction de la vegetation dans la savane de Lowveld en Afrique du Sud furent reunis pendant sept ans dans le but d'etablir l'etendue de leur impacte sur la couche herbacee restrictive. La classe de l'herbe, l'abondance et couverture furent examinees (450 zones; -4000 km^2). En se servant de l'ordination, la variation et les differences dans les variables de reponse-herbacee vis-avis de la composition perenne et la couverture a permis un regroupement environnemental general des zones avec un potentiel ecologique semblable. Nous montrons ici que les zones de fort potentiel ecologique supportent des plus fortes densites de grands carnivores, sans pour autant nuire a la composition de l'herbe et couverture. Les resultats ont des implications pour les utilisateurs de la terre et les responsables politiques par rapport a la creation d'une directive sur l'approvisionnement d'animaux.

Introduction

The Savanna Biome, (426,000 km^2 approximately 34%) of South Africa, is characterized by a grassy ground layer and distinct upper-layer of woody plants (Low & Rebelo, 1996). In the eastern Lowveld of this Biome, land-use practises have varied markedly over the last century, culminating in intensified multi-use exploitation of wildlife.

During the late 1800s wholesale destruction of wildlife