

RECOVERY, RESILIENCE AND STABILITY OF BIOSPHERE SYSTEMS IN THE KRUGER NATIONAL PARK

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PREFACE

The experimental work described in this dissertation was carried out in the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg, from January 2006 to December 2009, under the supervision of Professor Kevin Kirkman and co-supervised by Professor David Ward, Dr Mike Peel and Mr Craig Morris. These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others it is duly acknowledged in the text.

Signed:

K. J. Matchett (candidate).

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Professor Kevin Kirkman (supervisor).

FACULTY OF SCIENCE AND AGRICULTURE

DECLARATION 1 - PLAGIARISM

I, ...Katherine Jean Matchett....., declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
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 - a. Their words have been re-written but the general information attributed to them has been referenced
 - b. Where their exact words have been used, then their writing has been placed in italics and inside quotation marks, and referenced.
5. This thesis does not contain text, graphics or tables copied and pasted from the Internet, unless specifically acknowledged, and the source being detailed in the thesis and in the References sections.

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.....

FORMAT USED IN THESIS:

This thesis has been prepared as a series of four results chapters formatted as papers for submission to appropriate scientific journals, with a brief introductory chapter (Chapter 1) outlining the issues addressed in the research, a chapter describing the study site (Chapter 2) and a brief concluding chapter highlighting the main findings of the work (Chapter 7). Chapters 3 – 6 of this thesis have been prepared as papers for submission to scientific journals. There is thus some unavoidable repetition in the Introduction and Methods sections of these four chapters. The following journals have been selected for the submission of each chapter:

Chapter 3 – *Plant Ecology*

Chapter 4 – *Journal of Arid Environments*

Chapter 5 – *Austral Ecology*

Chapter 6 – *International Journal of Remote Sensing*

For consistency and readability, all four chapters in this thesis follow the format required for submission to *Austral Ecology*. The chapter numbers have been prefixed to all chapter sections, figures and tables, to avoid duplication in the dissertation. Chapters 3, 4 and 6 will be re-formatted before submission to the appropriate journals.

ROLE OF MY CO-AUTHORS:

For the four chapters (Chapters 3 – 6) intended for submission as papers to appropriate scientific journals, my four supervisors have been included as co-authors because of their significant scientific input. In all cases, I have been responsible for planning the experimental protocol and collecting and analyzing data, as well as interpreting the findings and writing the paper. My supervisors have given statistical advice and read successive manuscripts of the various chapters, making suggestions for improvement based on their areas of specialized knowledge.

Dr Ivan Thrash, who conducted the baseline study (1990) that formed the foundation for the comparisons made in this thesis, was contacted at the commencement of the study and asked to collaborate. He declined, and has made no scientific contribution to this thesis beyond that obtained from papers he authored and his PhD thesis, appropriately referenced in each chapter. Thus he was not given co-authorship of chapters 3 – 6.

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ABSTRACT

Water provision is an important tool in the management of savanna ecosystems. Artificial water sources are a potential focus for degradation (biodiversity and loss of ecosystem resilience at a range of spatio-temporal scales), because they alter plant-animal interactions and soil function and stability, through the creation of piospheres.

This study was undertaken as part of a drive by the Kruger National Park (KNP) to enable managers to integrate artificial waterhole management (e.g. waterhole closure or rotation) when setting goals for heterogeneity and biodiversity conservation in the park. The over-arching goal was to quantify the relationship between water provision and different attributes of heterogeneity, as part of a broader initiative to place water provision and piospheres within an ecosystem threshold framework.

Herbivore utilisation gradients (piospheres) around artificial waterholes in the KNP, described in 1990, were resurveyed in 2006-2007, against a backdrop of waterhole closure in the KNP, to contribute to an understanding of the factors governing recovery and resilience in grazing systems. The responses of the plant community and soil parameters to a relaxation of herbivore utilisation pressure around closed waterholes (recovering piospheres) were examined, as were changes in the same parameters at sites that have remained open (active piospheres). These ecosystem properties were considered in relation to structural and functional ecosystem thresholds, and the piospheres surveyed incorporated a range of rainfall and edaphic gradients in the KNP.

Herbaceous basal cover and soil infiltration capacity both increased significantly between 1990 and 2006/7, regardless of waterhole status. This was linked to higher rainfall in 2006/7, compared to 1990. The only vegetation variables to respond consistently to distance from water were the remote-sensed Normalized Difference Vegetation Index (NDVI) and herbaceous species composition. NDVI increased with distance from water, and annual grasses and forbs were most abundant close to water. Perennial, disturbance-sensitive climax species increased in abundance further from water. Soil analyses (N, P, pH, organic matter, and texture) and field measurements (infiltration, compaction) revealed no systematic piosphere patterns. Waterhole closure did not result in soil or vegetation recovery, but piosphere intermittency and the increases of basal cover and infiltration rate indicated that ecosystem resilience has not been compromised

by long-term artificial water provision in the KNP. This study has shown that the traditional piosphere model is of limited use in sub-humid savanna ecosystems like the KNP during above-average rainfall periods.

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CHAPTER 1: INTRODUCTION

Rangelands are economically and ecologically important systems in southern Africa. More than 75 % of the land area of South Africa is used for pastoral production (Tainton 1999) and conservation. Users of rangeland ecosystems include commercial and communal livestock producers, commercial game ranchers and private and governmental eco-tourism and conservation practitioners. These different users have fundamentally different management structures in place, with respect to animal type, diversity, stocking rates and products. They all, however, have a similar range of tools at their disposal with which to control how their animals utilize the rangeland. These include fences, fire, animal population control (culling or translocation) and water provision, all of which have important implications for animal movement patterns (Owen-Smith 1996; Smit *et al.* 2007).

Rangeland ecosystems in sub-Saharan Africa are subject to large climatic variation and frequent droughts. Water resources are frequently highly ephemeral and spatio-temporally unpredictable. The provision of artificial sources of perennial water for animal use has thus become a widespread and common practice, particularly in seasonally waterless areas where fences prevent herbivores migrating to reach alternative sources of drinking water. It is also, however, highly contentious, particularly in wildlife systems (Owen-Smith 1996; Smit *et al.* 2007), and has far-reaching implications for rangeland degradation, including a perceived loss of biodiversity (James *et al.* 1999; Smit *et al.* 2007), productivity (Thrash 1993; Parker & Witkowski 1999) and ecosystem resilience (Smit *et al.* 2007) and stability.

The provision of artificial water affects all ecosystem properties, because it changes the way in which animals utilize the rangeland. If correctly managed, it can promote animal production and contribute to rangeland heterogeneity (e.g. habitat diversity, plant species diversity and structural vegetation diversity) at a range of scales (Adler *et al.* 2001; Gaylard *et al.* 2003; Chamaille-James *et al.* 2009). Water provision causes water-dependent animals to concentrate around the focal points in the landscape where drinking water is available. Consequently, it changes the spatial distribution of animal impacts on the rangeland. Such impacts include trampling, dung and urine deposition, the dispersal of seeds, plant biomass removal and the redistribution of nutrients. The result can be large changes to soil chemical and physical properties and vegetation composition and structure. Artificial water provision can therefore potentially result in localised degradation (James *et al.* 1999; Gaylard *et al.*

2003; Nangula & Oba 2004). If widespread, the rangeland may experience losses of ecosystem heterogeneity, resilience and function.

Abiotic factors such as geology, topography and rainfall variability are the principal factors determining patterns in semi-arid vegetation, but herbivore impacts (grazing, trampling, nutrient redistribution) also create and maintain spatial heterogeneity and pattern at a range of spatial scales (Derry 2004). The gradients of animal impact associated with artificial water provision provide a model system in which to examine these effects.

Ecologists have studied these gradients in a range of savanna and grassland ecosystems (Osborn *et al.* 1932; Lange 1969; Graetz & Ludwig 1978; Andrew & Lange 1986; Andrew 1988; Thrash 1993; Derry 2004; Smet & Ward 2005). The temporal variability of piosphere systems is not as well understood (Adler & Hall 2005), and the response of the vegetation and soil parameters within piosphere systems to the closure of waterholes is relatively unknown.

2.1 Kruger National Park

The Kruger National Park (KNP) is one of the largest national parks in the world (18 989 km²) and incorporates a range of savanna landscapes. It has been the subject of much debate and research into the effects of water provision in the KNP (Gaylard *et al.* 2003). Between the mid-1930s and the late-1970s, artificial water sources were established throughout the park. The goal was to stabilise perennial water availability in order to reduce the impact of severe droughts on herbivore population dynamics (van der Schijff 1959; Pienaar 1983; Joubert 1986; Thrash 1993; Thrash *et al.* 1993a; Thrash 2000; Gaylard *et al.* 2003). By 1990, less than 20 % of the land area of KNP was further than 5 km from perennial water, even during severe droughts (Gaylard *et al.* 2003). In spite of this, the anticipated benefits of water provision, such as herbivore population stabilization, were not forthcoming, and research had indicated that the uniform herbivore utilization that had resulted from the water provision programme had caused a loss of rangeland diversity (van der Schijff 1959; Thrash 1993; Gaylard *et al.* 2003). Negative effects of artificial water provision included starvation and mortality of wildlife during droughts (Walker *et al.* 1987; Knight 1995). Altered predator-prey dynamics develop, to the detriment of rare prey species such as roan and sable antelope (Harrington *et al.* 1999; Grant *et al.* 2002), and the perceived loss of vegetation diversity and productivity has been noted in a number of studies (Thrash *et al.* 1991b; a; Thrash 1993; Thrash *et al.* 1993b; Clegg 1999; Heshmatti *et al.* 2002; Derry 2004; Todd 2006). By the mid-1990s, the KNP had seen a shift in management policy, which now

aimed to minimize human intervention and promote savanna heterogeneity at a range of spatio-temporal scales and conserve ecosystem resilience (the ability of the ecosystem to absorb disturbance without changing state (Gunderson 2000; Gunderson & Holling 2002; Rogers 2003). Consequently, the closure of waterholes commenced in the late-1990s (Pienaar *et al.* 1997). This followed recommendations that waterholes should be spaced no closer than 15 km apart (Owen-Smith 1996) and that large areas of the park be maintained without artificial water provision, in line with other studies that have explored the benefits of water-remoteness for grazing-sensitive plant species (James *et al.* 1999; Landsberg *et al.* 2003; Fensham & Fairfax 2008).

The current study continues an investigation of the effects of water provision on soil and vegetation properties conducted in the early 1990s (Thrash *et al.* 1991b; a; Thrash 1993; Thrash *et al.* 1993b; a; 1995; Thrash 1997; 1998a; b; 2000), after closure of a number of waterholes. I re-examined vegetation and soil parameters along herbivore utilization gradients around waterholes documented in 1990 (Thrash *et al.* 1991b; a; Thrash 1993; Thrash *et al.* 1993b; a; 1995; Thrash 1997; 1998a; b; 2000), in 2006 and 2007. Approximately 35 % of these waterholes had been inactive since 1999/2000, and the remainder remained active during the study period.

The objectives of the study were to:

1. Survey herbivore utilization gradients around the same waterholes examined in 1990.
2. Document spatial vegetation and soil patterns and compare them to the situation in 1990 (i.e. spatio-temporal ecosystem dynamics within the context of water provision).
3. Relate the patterns of recovery at closed-waterhole sites and temporal vegetation change at active waterhole sites (since 1990) to abiotic (rainfall, soil type) and management (fire) factors.
4. Investigate the effectiveness of waterhole closure with respect to the Kruger National Park's management goals of maintaining rangeland resilience and promoting heterogeneity and biodiversity.

This thesis thus addressed the following key research questions:

1. How does the plant community (grasses, forbs and woody species composition, structure and productivity) respond to disturbance by ungulate herbivores associated with open waterholes, in the medium- to long-term? This is addressed in Chapter 3.

2. How does vegetation composition and structure change after waterhole closure? This is addressed in Chapter 3.
3. What impact do waterholes have on soil productivity and function (soil nutrient status, compaction, soil texture, infiltration capacity) in the medium-to-long term, and does waterhole closure alter these patterns? This is addressed in Chapter 4.
4. What patterns of patch structure (vertical and horizontal) develop along distance-from-water gradients? This is addressed in Chapter 5.
5. Can remotely-sensed vegetation indices (e.g. Normalized Difference Vegetation Index) be used to detect and compare piospheres at a landscape scale? Addressed in Chapter 6.
6. How do environmental and management factors (e.g. rainfall and waterhole status) affect recovery and stability along herbivore utilization gradients? This is addressed in Chapters 3 – 6.
7. Is the current waterhole closure policy redressing the loss of rangeland heterogeneity experienced after water provision? This is addressed in Chapters 3 -6.

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CHAPTER 2: DESCRIPTION OF STUDY SITE

2.1 THE ABIOTIC TEMPLATE OF THE KRUGER NATIONAL PARK (KNP)

Topography

The KNP is in the north-eastern Lowveld of South Africa, and is bounded on the east and west by the Lebombo Mountains and the coastal floodplains of Mozambique, and the Drakensberg mountains, respectively. The Lowveld of South Africa is located in the north-eastern corner of South Africa, east of the foothills of the Drakensberg escarpment, in the Mpumalanga and Limpopo provinces. The Lowveld on average lies approximately 300 m above sea level (Venter *et al.* 2003), and slopes gently down towards the east.

Climate

The KNP is divided into two broad climatic zones (Weather-Bureau 1986; Venter *et al.* 2003): the Lowveld-bushveld zone incorporating the southern and central regions of the park, and the northern arid-bushveld zone in the north. The Lowveld bushveld zone receives 500 - 700 mm of rainfall annually and experiences evaporation of 6 mm per day (October), whereas the northern arid bushveld zone receives 300 - 500 mm per year, and potential evaporation is 7 mm/day (October) (Venter *et al.* 2003). Both zones experience high summer temperatures and humidity and mild, frost-free winters. Rainfall is highly seasonal, with most of the annual rainfall falling between October and April.

Savannas in the Kruger National Park may be classified as sub-humid, because they have a distinct dry season, with only about 5 mm of rain per month between June and August (Rutherford *et al.* 2006). A north-south rainfall gradient operates over the KNP, with the southern reaches of the park experiencing higher mean annual rainfall and lower coefficients of inter-annual rainfall variation (25 % in the south and 35 % in the north) than the northern regions (Venter *et al.* 2003). A lesser rainfall gradient operates from east to west over the KNP, with the western regions receiving higher rainfall compared to the east (orthographic rainfall gradient) (Venter *et al.* 2003). Approximately 20 % of rainfall years in the KNP are classifiable as drought years, if a drought is a year with less than 50 % of the long-term mean annual rainfall (Venter *et al.* 2003). There have been no overall trends in rainfall over the past two decades, but the pattern is one of clear periods of below-average rainfall alternating with periods of above-average rainfall, linked to El Niño-Southern Oscillation events (Tyson

1985; Tyson & Preston-Whyte 2000). Rainfall in the KNP typically occurs as discrete events (thunderstorms), and rainfall intensity is thus high (Venter *et al.* 2003).

The stochasticity of the KNP's rainfall and the high evaporative potentials result in pulsed biological activity in the soil and vegetation (Venter *et al.* 2003). Biota are very active for short periods immediately following rainfall events, after which they enter a phase of relative inactivity.

There is a slight north-south temperature gradient across the park, with the northern regions experiencing higher maxima than the southern regions. Occasional, mild frosts do occur in the hilly areas of the southern region, but are rare in the north. Humidity in the KNP is fairly low, with summer humidity remaining between 50 and 53 % on average, and winter humidity between 37 and 42 % (Venter *et al.* 2003). Low winter humidity contributes to the KNP being a fire-prone system.

Geology

The KNP can be divided into eastern and western landscapes on the basis of the underlying geology: the eastern half of the park is characterized by basaltic rock, and the western half by granitic rock (Venter *et al.* 2003). A band of sedimentary rock, running along a north-south axis, separates these two major geological landscapes.

Soils

Soils tend to become deeper as rainfall increases along a north-south gradient in the KNP, with soil profiles in the Pretoriuskop area an average of 150 cm deep, and soils north of Phalaborwa only 30 cm deep (Venter *et al.* 2003). This gradient is stronger for granite-derived soils than for basaltic soils. Soil type diversity also declines from the south to the north. Soils in the north experience relatively less leaching than soils in the south of the park, and are also more abundant in calcium carbonate (Venter *et al.* 2003).

Vegetation

On a very broad scale, vegetation in the more arid northern KNP tends to be dominated by *Colophospermum mopane*, and vegetation in the south is more variable. Hilltops on granitic soils tend to support unpalatable grasses, whereas the bottomlands have a more palatable suite of grasses. These areas attract low and moderate herbivore biomasses respectively. The basaltic soils are typified by palatable grasses and high herbivore biomass. The soil and vegetation on the basaltic soils have a high nitrogen content, whereas on the granites, the

crests have low nitrogen availability and the foot-slopes high nitrogen availability (Venter *et al.* 2003).

The savanna types in the KNP can be broadly classified as dystrophic or eutrophic, (Venter *et al.* 2003). Savannas on the nutrient-poor granite-derived soils tend to be dominated by *Combretum* and *Terminalia* tree species and trees of the family Caesalpiniaceae, and are associated with short, wiry, unpalatable grass species such as *Aristida* spp., *Eragrostis* spp. and *Pogonarthria squarrosa* – all fairly disturbance-tolerant species, many of which are annual pioneers. Savannas on the nutrient-rich basaltic soils are dominated by *Acacia* tree species and a palatable, taller and more grazing-sensitive and perennial suite of tufted grasses, including *Themeda triandra*, *Panicum maximum* and *Urochloa mosambicensis*. Rutherford *et al.* (2006) broadly describe all the savanna types in the KNP as either Mopane bushveld (the areas north of the Olifants River) or Lowveld Bushveld (south of the Olifants River).

2.2 LAND SYSTEMS AND SITE SELECTION

The highly heterogeneous abiotic template of the KNP has produced a highly variable vegetation pattern. The KNP is divided into 11 land systems (based on similar geology, geomorphology and climate) and 56 land types (recurring soil patterns associated with catenal position) based on geology, topography, rainfall, soils and woody vegetation, from the work of Venter (1990) and Gertenbach (1983). On a finer scale, land types incorporate land units (soil types with similar properties and specific vegetation associations e.g. riverine vegetation) and land elements (sodic patches, specific species associations). In this study, waterholes in the Skukuza, Satara, Phalaborwa, and Letaba land systems were surveyed (Figure 2.1). Brief descriptions (Venter *et al.* 2003) of these areas follow:

Skukuza and Phalaborwa Land Systems

Both these land systems are underlain by granitic rocks and are typified by very distinctive catenal gradients of soil type. In the Skukuza land system, the vegetation of the sandy uplands included dense sands of deciduous *Combretum* spp. and *Terminalia* spp. The foot-slopes, where duplex soils are common, are characterised by more open, small-leaved, thorny shrub, in which several species of *Acacia* and *Albizia* occur along with *Dichrostachys cinerea*, *Euclea* spp., and *Combretum hereroense*. Grasses abundant on the foot-slopes tend to be nutritious bulk-growers. Seep-lines are dominated by *Terminalia sericea* and *Combretum zeyheri*, and water-loving sedges and grasses such as *Eragrostis gummiflua*.

Grass cover in the land system as a whole tends to be sparse, especially in dry years, but may be moderate to dense in wet periods.

The Phalaborwa land system is characterised by *Combretum apiculatum* and *Colophospermum mopane* bushveld. *C. apiculatum* typically occurs on the shallow gravels and sandy soils on the crests, whereas *C. mopane* grows in the clayey soils of the foot-slopes (duplex soils) and along dolerite dykes.

The Satara and Letaba Land Systems

These two areas are characterised by clayey soils derived from the weathering of basic igneous rock (basalt). The Satara land system consists of fine-leafed tree savanna dominated by *Acacia nigrescens*, *Dichrostachys cinerea* and *Sclerocarya birrea*. The Letaba system is associated with *Colophospermum mopane* shrub-veld, although *Combretum imberbe* is also abundant. The Satara land system receives higher rainfall than the Letaba system, and is thus characterised by higher perennial grass cover.

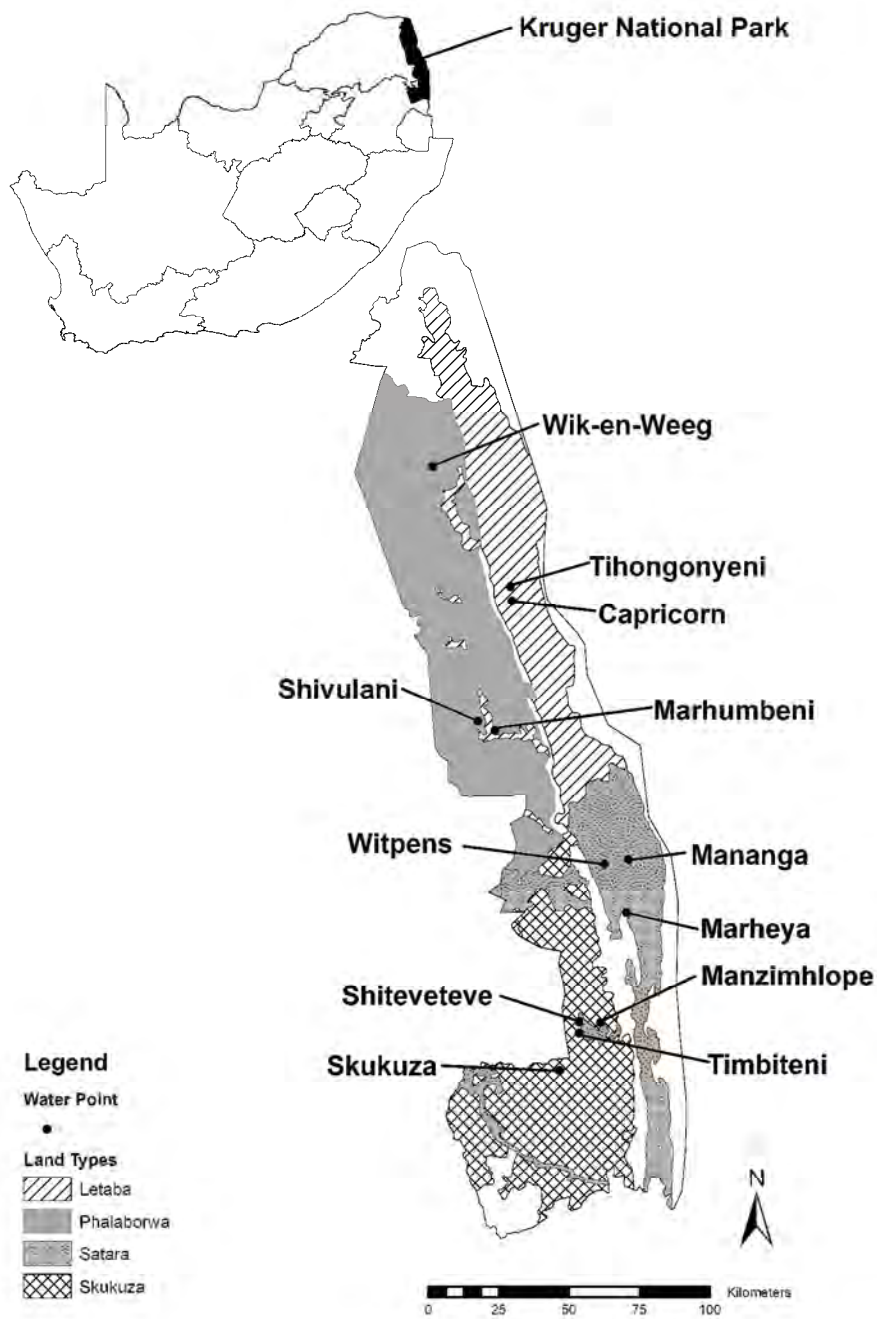


Fig. 2.1: The Kruger National Park, South Africa, showing the distribution of sample sites in each region. The Skukuza and Phalaborwa regions are on granitic soils, the Satara and Letaba regions are dominated by basalts.

Vegetation and soil parameters were measured along distance-from-water gradients associated with the following waterholes (Fig. 2.1): Timbiteni, Shiteve-teve and Manzimhlope in the Tshokwane game ranger section (Skukuza land type), Witpens, Mananga and Marheya in the Satara section (Satara land type), Capricorn and Tihongonyeni in the Mooiplaas section (Letaba land type), Marhumbeni and Shivulani (Phalaborwa region and land type) and Wik-en-Weeg (Woodlands region, Phalaborwa land type). The dates on which the waterholes were established are summarised in Table 2.1. These eleven waterholes were selected because they were surveyed in detail in 1990 by Thrash (1993), and baseline vegetation and soil data was thus available from which to assess recovery. The selection of these sites has resulted in an unbalanced study design, because 7 open and only four closed waterholes are surveyed.

Table 2.1. The dates (month and year) of opening and closure of the eleven artificial waterholes surveyed in 2006, with current status given

Land type	Section	Site	Current status	Date opened	Date closed
Skukuza	Tshokwane	Manzimhlope	Open	01/1933	
		Timbiteni	Open	01/1962	
		Shiteve-teve	Open	05/1973	
Satara	Satara	Witpens	Open	unknown	
		Mananga	Open	07/1973	
		Marheya	Closed	07/1962	Structure removed 2001
Phalaborwa	Phalaborwa	Shivulani	Open	01/1935	
		Marhumbeni	Closed	07/1970	Structure removed 2001
	Woodlands	Wik-en-Weeg	Closed	1973	Unknown (assumed 2001)
Letaba	Mooiplaas	Capricorn	Closed	02/1975	Original structure removed 2001, roan enclosure completed 2002. Waterhole reopened 2002.
		Tihongonyeni	Open	04/1962	

The following waterholes were closed (as of 1999/2000): Marheya, Marhumbeni and Wik-en-Weeg. The Capricorn waterhole was initially closed in 2001, after which a rare-

antelope enclosure was erected at the site, whereupon the waterhole was re-opened. For the purposes of this study, we have regarded this waterhole as closed, because it falls within the rare-antelope enclosure and is thus isolated from general herbivore use. The other waterholes remain active, because the boreholes are open. We refer to waterholes/study sites as open (borehole functional) or closed (borehole non-functional). Wildlife still has access to closed waterholes – i.e. herbivores are not excluded from these sites, although the borehole does not actively pump water for their use.

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CHAPTER 3: VEGETATION GRADIENTS AROUND OPEN AND CLOSED WATERHOLES IN THE KRUGER NATIONAL PARK

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Abstract Modern protected area management focuses on conserving ecosystem heterogeneity at all spatio-temporal scales, because it is the basis for maintaining resilience. We examined herbaceous and woody vegetation compositional and structural patterns in piospheres around open and closed waterholes in the Kruger National Park. Data collected in 1990, when all the waterholes were open, were compared to the situation in 2006, six years post-closure. We found that herbaceous basal cover and biomass increased significantly between the two study periods, but found no effect of waterhole closure. There were increases in the relative abundance of grazing-tolerant grass species at all waterholes, regardless of waterhole status. We detected no effect of waterhole closure on herbaceous species composition. We found no piosphere patterns in the woody community. We concluded that grazing has a strong, long-term effect on the composition of the herbaceous community, but that rainfall is more important in determining cover and biomass. We also concluded that herbivores consuming woody plants (browsers) are not creating piospheres in the woody community, because they are more water-independent than grazers and are not as strongly associated with artificial waterholes.

Key words: piosphere, resilience, recovery, cover, community composition

3.1 INTRODUCTION

Vegetation patterns in piospheres

Within a rangeland, water-dependent herbivores move frequently between foraging and drinking stations. Their foraging pressure is thus concentrated around waterholes (Lange 1969; Andrew & Lange 1986; Andrew 1988; Derry 2004), creating gradients of attenuating impact called 'piospheres' (Osborn *et al.* 1932; Valentine 1947; Lange 1969).

Piospheres are important as potential foci for localized degradation (Thrash 1993; Thrash & Derry 1999; Derry 2004). They can either cause landscape-scale biodiversity losses when artificial water-points are insufficiently dispersed in the landscape (Collinson 1983), or contribute to biodiversity and landscape heterogeneity when properly managed and properly spaced (van der Schijff 1959; Gaylard *et al.* 2003; Chamaille-James *et al.* 2009).

Plant responses within a piosphere are a function of local edaphic, climatic and disturbance (e.g. fire, grazing) factors (Kalikawa 1990; Thrash 1993; Makhabu *et al.* 2002; Derry 2004). These responses affect the outcome of plant competition for light, space, nutrients and moisture (Milchunas *et al.* 1988) and cause compositional changes along the distance-from-water gradient (Thrash 1993). The life history traits of different species determine their positions along the grazing pressure gradient (Laihacar *et al.* 1993). Herbivore disturbance within the piosphere strongly influences the outcome of plant competitive changes, by promoting grazing tolerance or suppressing recruitment and growth of grazing-intolerant species (Andrew & Lange 1986; Thrash 1993; Clegg 1999; Smet & Ward 2005).

At the centre of a piosphere, heavy trampling frequently produces a zone denuded of vegetation (Graetz & Ludwig 1978; Andrew 1988), and is often termed the 'sacrifice zone' (Thrash & Derry 1999; Derry 2004). Immediately beyond this, a zone characterized by a short sward of annual species occurs, followed by an area dominated by taller annuals and some perennials and eventually replaced by a zone dominated by grazing-intolerant perennial grasses (Friedel 1988; Thrash 1993; James *et al.* 1999).

Piosphere patterns have also been recorded in the woody community in many savanna ecosystems where water is artificially supplemented (Tolsma *et al.* 1987; Smet & Ward 2005; Fornara & Du Toit 2007). Woody plants sensitive to browsing often experience increased mortality close to waterholes, and are replaced by browse-tolerant species (Andrew & Lange 1986; Friedel 1988; Thrash *et al.* 1991; Bastin *et al.* 1993). Heavy grazing near waterholes alters

the outcome of tree-grass competition, leading to increases in the density of trees and shrubs near waterholes (Friedel 1988; Thrash *et al.* 1991; Perkins & Thomas 1993). Fornara and Du Toit (2007) documented 'browsing lawns' around artificial waterholes in the Kruger National Park (KNP). They found that repeatedly browsed trees near waterholes developed browse-resistance or browse-tolerance traits at the expense of reproductive success. Milton (1991) also found that woody plants in drainage lines and pans favoured by browsing mammals developed spinescence to resist browsers. High soil nutrient availability near artificial waterholes also promoted coppicing in browsed trees, and increased the palatability of trees close to water (Du Toit *et al.* 1990; Fornara & Du Toit 2007).

Piospheres in the Kruger National Park

Artificial water provision began in the KNP in the 1930s (Joubert 1986). The goal of artificial water provision was to minimize the effects of temporal rainfall variability and low perennial water source density by supporting herbivore populations through droughts. By 1995, less than 20 % of the landscape in KNP was further than 5 km from water (Gaylard *et al.* 2003).

The anticipated benefits of the water-for-game programme were not forthcoming (Gaylard *et al.* 2003). A reversal of the water provision policy in the KNP was initiated in the mid-1990s (Pienaar *et al.* 1997), and a proportion of the artificial water-points in the park was closed, providing an ideal opportunity to study the recovery and stability of piosphere systems. In addition, the ecological management of the KNP has become more orientated towards promoting biodiversity at all scales (genetic, species, habitat, landscape, etc), and maintaining ecosystem resilience in the long-term (Rogers 2003). We examined spatio-temporal vegetation patterns associated with piospheres, in an attempt to understand how piospheres degrade.

This study also aimed to quantify spatio-temporal changes to herbaceous vegetation composition and structure associated with the same piospheres described in 1990 (Thrash 1993). We hypothesize that vegetation indicators such as plant species composition, as well as woody plant density and basal cover will show recovery around closed waterholes, and that piospheres around open waterholes will have expanded since 1990.

3.2 METHODS

Study sites

The four major land systems in the KNP are the Skukuza, Satara, Phalaborwa and Letaba land systems (Venter 1990). The impact of ungulate herbivores on herbaceous and woody vegetation was sampled at eleven waterholes in April/May 1990 (Fig 2.1). These eleven waterholes were revisited in April/May 2006. These sites included 7 open and 4 closed waterholes. At waterholes referred to as closed, the windmills have been disabled and water is no longer pumped into the waterhole/trough. Animals still have access to these sites – no herbivore exclusion has been implemented. The land systems in which each site occurs and the current status of each waterhole are summarized in Table 3.1.

The Skukuza and Phalaborwa land systems are underlain by granitic rocks and are characterized by distinctive catenal soil gradients. In the Skukuza land system, the vegetation of the sandy uplands includes dense sands of deciduous *Combretum* spp. and *Terminalia* spp. The foot-slopes, where duplex soils are common, are characterised by more open, small-leaved, thorny shrub, in which several species of *Acacia* and *Albizia* occur along with *Dichrostachys cinerea*, *Euclea* spp., and *Combretum hereroense*. Grasses abundant on the foot-slopes tend to be nutritious bulk-growers. Seep-lines are dominated by *Terminalia sericea* and *Combretum zeyheri*, and water-loving sedges and grasses such as *Eragrostis gummiflua*. Grass cover in the land system as a whole tends to be sparse, especially in dry years, but may be moderate to dense in wet periods.

The Phalaborwa land system is characterized by *Combretum apiculatum* and *Colophospermum mopane* bushveld. *C. apiculatum* typically occurs on the shallow gravels and sandy soils on the crests, whereas *C. mopane* grows in the clayey soils of the foot-slopes (duplex soils) and along dolerite dykes.

The Satara and Letaba land systems are characterized by clayey soils derived from the weathering of basic igneous rock (basalt). The Satara land system consists of fine-leaved tree savanna dominated by *Acacia nigrescens*, *Dichrostachys cinerea* and *Sclerocarya birrea*. The Letaba system is associated with *Colophospermum mopane* shrub-veld, although *Combretum imberbe* is also abundant. The Satara land system receives higher rainfall than the Letaba system, and is thus characterized by higher perennial grass cover.

Table 3.1. The dates (month and year) of opening and closure of the eleven artificial waterholes surveyed in 2006, with current status given

Land type	Site	Current status	Date opened	Date closed
Skukuza	Manzimhlope	Open	01/1933	
	Timbiteni	Open	01/1962	
	Shiteve-teve	Open	05/1973	
Satara	Witpens	Open	unknown	
	Mananga	Open	07/1973	
	Marheya	Closed	07/1962	Structure removed 2001
Phalaborwa	Shivulani	Open	01/1935	
	Marhumbeni	Closed	07/1970	Structure removed 2001
	Wik-en-Weeg	Closed	1973	Unknown (assumed 2001)
Letaba	Capricorn	Closed	02/1975	Structure removed 2001, roan enclosure completed 2002. Waterhole reopened 2002.
	Tihongonyeni	Open	04/1962	

Field data collection

Herbaceous basal cover, biomass and species composition

We sampled herbaceous species composition in April-May 2006, using the same method employed by Thrash (1993), i.e. four parallel transects within a 5 m belt were established at each waterhole, beginning at the edge of the waterhole and extending to 5000 m. Transects were orientated to avoid large catenal changes, roads and drainage lines. Measurements were taken at 1 m intervals between 0 and 150 m, 500 and 510 m, 1000 and 1010 m, 2000 and 2010 m and 5000 and 5010 m. A nearest-plant technique (Mentis 1981; Barnes 1990; Thrash 1993) was used, for which the species rooted closest to the transect line at each sampling point was identified (Cottam & Curtis 1956; Thrash 1993). After combining data for 10 m transect segments (40 sampling points), we calculated the relative contribution of each species to overall composition. Grasses were identified to species level (Gibbs-Russell *et al.* 1990), but non-grasses were grouped as “forbs” and “sedges”.

The herbaceous basal cover (%) within each transect and plot was also measured, using a point-distance (nearest individual) technique developed by Cottam and Curtis (1956). At each point the distance to the base of the nearest plant, and its diameter, were recorded. Mean distance to the nearest plant and mean basal diameters were used to determine basal cover (Cottam and Curtis 1956) for the 10 m transect segments. Basal cover was similarly measured in 1990 (Thrash 1993).

Herbaceous biomass was measured along the same 5 m by 5000 m transect using a disk pasture meter (Bransby & Tainton 1977). Measurements were made at 0.5 m intervals along 5 parallel transects spaced 1 m apart. Data from each 10 m (100 points) segment were combined and compressed vegetation height (mean disk height) was then used in the following equation, developed for the KNP (Trollope & Potgieter 1986), to calculate herbaceous standing crop (dry mass of standing herbaceous material per unit area, excluding litter):

$$y = (2260 \cdot x^{0.5}) - 3019,$$

where y = herbaceous standing crop ($\text{kg}\cdot\text{ha}^{-1}$) and x = mean disc height (cm).

Woody species composition and structure

Belt transects (10 X 50 m) were placed perpendicular to the main 5 m by 5000 m transect at each waterhole, at 25, 50, 75, 100, 200, 300, 400, 500, 1000, 2000 and 5000 m from the waterhole. Within each belt transect, we identified all the woody plants (trees and shrubs) to species and recorded their heights (m).

Data Analysis

Herbaceous basal cover, biomass and species composition

For both study periods (1990 and 2006), data from the 10 m sampling segments were ordinated (ter Braak & Smilauer 1997) using Detrended Correspondence Analysis (DCA) (Hill & Gauch 1980). Rare species were down-weighted. Individual samples (sites) with rare species can distort the analysis; thus the rare species are given a lower weight than the common species, but still retained in the analysis. The abundance of rare species is reduced (down-weighted) in proportion to their abundance. Species with a frequency of less than 20 % of the frequency of the most common species are deemed “rare” (Ter Braak & Smilauer 2002). Patterns of zonation along distance-from-water gradients at each site were inferred from the clustering of sample plots in

ordination space following DCA, and subjectively positioned circles were plotted on the graphs to distinguish between zones at each site.

The datasets from 1990 and 2006 were then combined. Using dummy variables to code for site, a Canonical Correspondence Analysis (CCA) was run to test for an overall effect of distance and time (1990 and 2006), and their interaction. CCA is a constrained ordination technique, because the relative position of the sites and species in the ordination plot is influenced (constrained) by a set of covariates, usually environmental variables recorded for each sampling unit (Quinn & Keough 2002). In this case, the environmental variables used were distance from the waterhole (m), time (1990 versus 2006) and their interaction (distance X time). Time was treated as a nominal variable. Rare species were down-weighted. Monte Carlo permutation tests were used to test the significance of distance and time effects and interactions for each site.

A blocked multi-response permutation procedure (MRPP) (McCune & Mefford 1999) was used to investigate the effect of waterhole closure on the relative amount of species compositional change between 1990 and 2007, treating distance classes as blocks. MRPP (Mielke *et al.* 1976; Zimmerman *et al.* 1985) tests hypotheses about group differences in Euclidean distances. MRPP determines the mean of the Euclidean distances between objects within groups and calculates an MRPP statistic (δ) that is a linear combination of the mean within-group Euclidean distances. Delta (δ) represents a weighted average, based on sample size, of the within-group mean Euclidean distances. MRPP is thus a method of quantifying group dissimilarities. Chance-correlated, within-group agreement values (A , a descriptor of within-group homogeneity compared to the random expectation) were also calculated for each waterhole. The T-statistics (difference between observed and expected δ , where δ is the average distance between blocks, within treatments) were grouped according to waterhole status, and open and closed sites compared. The Euclidean Distance (ED) between the compositional scores (DCA axis 1 scores) for 1990 and 2006 were calculated (Primer 2006) for each distance class, and plotted against distance-from-water for the individual sites, so that the positions of the biggest changes in composition from 1990 to 2006 (between blocks) at each site could be determined. The mean compositional heterogeneity of each site for 1990 and 2006 was calculated based on the Euclidean distances between distance classes at a site within blocks.

These values were compared using one-way ANOVA with time as a factor with two levels. The assumptions of ANOVA (normality and homogeneity of variance) were met.

We calculated Bray-Curtis dissimilarity values, based on herbaceous species composition, for each 10 m transect segment (plot), compared with each other segment, and determined the proportion of comparisons with values < 0.25 (i.e. low heterogeneity) and > 0.75 (high heterogeneity). We also calculated Shannon's diversity and equitability for each 10 m transect segment.

Species were placed into functional groups: forbs, sedges, grazing-sensitive decreaseers, species abundant in under-grazed veld (increaser I's), and grazing-tolerant increaser II/III's (Dyksterhuis 1949; Van Oudtshoorn 2002). The difference (2006 – 1990) in the % contribution of each plant functional group between years was plotted against distance from water. Positive values indicated an increase in the contribution of a plant functional group, and negative values a decrease thereof.

The responses of herbaceous basal cover and biomass to distance from water were determined using generalized additive models (GAMs). GAMs (Hastie & Tibshirani 1990) incorporate properties of generalized linear models (GLMs) and additive models (Quinn & Keough 2002). Each predictor is a non-parametric smoothing function, and scatter-plot smoothers such as Lowess or cubic splines are used to obtain smooth generalizations of the relationship between predictor and response variables (Hastie & Tibshirani 1990; Quinn & Keough 2002). Various distributions for the dependent variable are allowed, and different functions can be used to link the expected values of the dependent variable and the values of the predictor variable. Our data had a normal distribution and we therefore used an identity link function. Models with up to three smoothing functions were considered, and Akaike Information Criteria (AIC) were used to select the best-fit model (Akaike 1973; Buckland *et al.* 1993; Anderson & Burnham 2000). GAMs were fitted for both 1990 and 2006.

Woody species composition and structure

Woody plants were categorized into five height classes (< 1 m, 1 – 2 m, 2 – 4 m, 4 – 6 m and > 6 m), and both the overall woody plant density (no. woody plants/km²) and the density of woody plants within each tree height class was calculated, for each distance from water. GAMs of the change in woody plant density along the distance-from-water gradient at each site were

fitted (ter Braak & Smilauer 1997) for each tree height class, and overall, for all the height classes combined.

Bray-Curtis dissimilarity indices were used to analyze the structural diversity of each piosphere. At each site, dissimilarity values were calculated for each distance class, and compared to each other distance class, for the abundance of trees in each of the five height classes. The proportion of pairs with Bray-Curtis values < 0.25 and > 0.75 were then compared for the eleven sites.

The species composition data were used to calculate the expected density of individuals of each species, at each distance from water. After \log_{10} transformation, we subjected these compositional data to CCA, with distance from water (\log_{10} -transformed) as the sole environmental variable (ter Braak & Smilauer 1997). We performed separate analyses for each site. Rare species were down-weighted, and Monte Carlo permutation tests used to calculate the significance of the first canonical ordination axis in each case.

We also used Bray-Curtis dissimilarity values to analyze the compositional heterogeneity of each site, using the identical method to that described for structural diversity indicated above. Shannon's diversity index (H') and equitability (J) were also calculated for each distance from water class at the eleven sample sites, using the following equations:

$$H' = \sum P_i \ln P_i, \text{ for } S \text{ species, and } J = H'/\ln S,$$

where S = total no. species in the community and P_i = proportional contribution of the i^{th} species to the community. Paired sample t-tests were used to compare diversity at open and closed sites.

Open versus closed waterholes

We compared open and closed sites for all variables, for both 1990 (all sites open) and 2006 (some sites closed) by calculating the area under the curve (AUC) for each site. Because GAMs could not be fitted to all sites for all variables, AUC was calculated from a scatter plot of the data (i.e. not using the fitted models). The AUC represented a single, integrated value for each site, taking distance from water into account. Open and closed waterholes were compared using a t-test (equal variances not assumed) for each variable.

Comparison between sampling periods

For all vegetation variables sampled in 1990, comparisons between 1990 and 2006 were made using paired-sample t-tests. For each distance from water at each site, the value recorded in 1990 was compared to that recorded in 2006.

3.3 RESULTS

Herbaceous species composition

Clear piosphere patterns were found for herbaceous species composition in both 1990 and 2006, for most sites (Fig. 3.1 and 3.2). The biplots shown are from the Marheya waterhole in 1990 and 2006. The patterns found at the 11 waterholes were very similar, and these two examples have been chosen as representative of the general pattern in the two periods. In 1990, plots close to the waterholes (0 – 50 m) were typified by high abundances of forbs, *Tragus berteronianus*, and *Eragrostis* spp. At intermediate distances from water (50 – 150 m), *Dactyloctenium aegyptium*, *Urochloa mosambicensis* and *Chloris virgata* were common. The plots 500 – 5000 m from water tended to be associated with palatable, grazing-sensitive species such as *Themeda triandra* and *Digitaria eriantha*. Only the first two of these zones present in 1990 were represented in 2006.

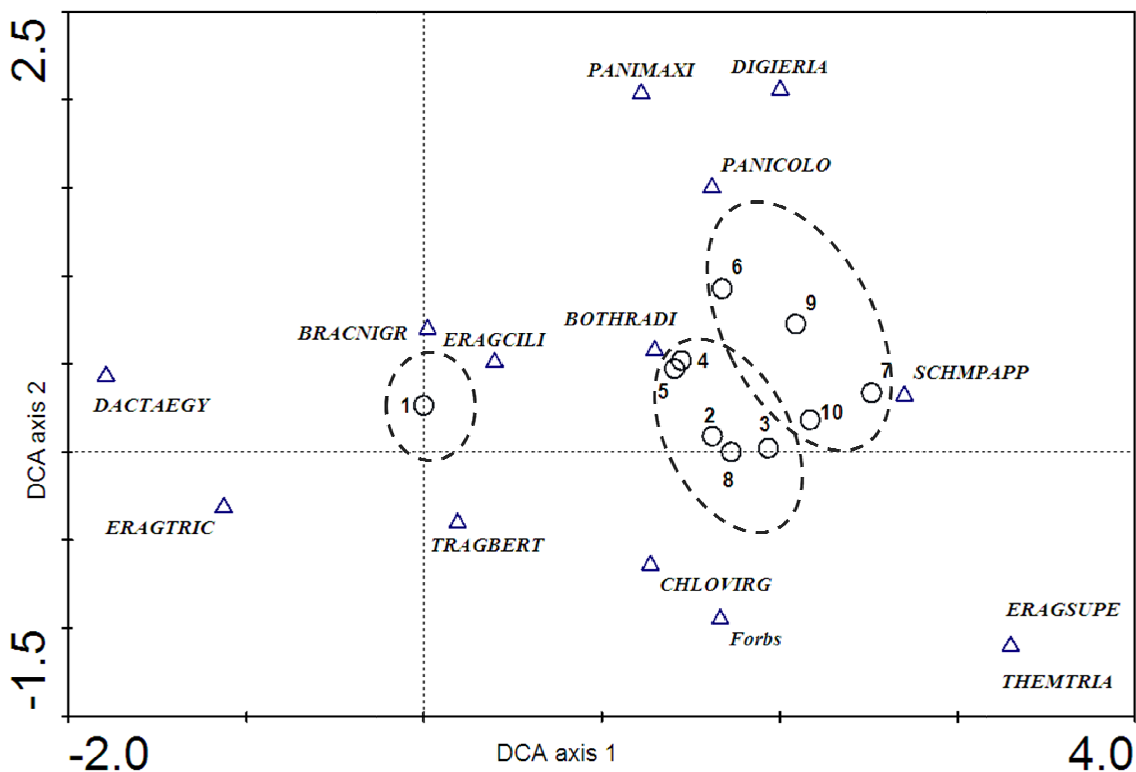


Fig. 3.1. First and second axes of a detrended correspondence analysis (DCA) of herbaceous species composition data along a distance-from-water gradient at Marheya waterhole (1990). The eigenvalues for DC axes 1 and 2 were 0.371 and 0.095, respectively. The two axes together accounted for 52.0 % of the variation in species composition. Species abbreviations are tabulated (Table 3.2) in Appendix A. Circles represent sites; triangles represent species. Sites with small numbers are close to the waterhole, those with larger numbers are further from the waterhole (1 = 1 – 10 m, 2 = 10 - 20 m, 3 = 20 – 30 m, 4 = 30 – 40 m, 5 = 50 – 60 m, 6 = 60 – 70 m, 7 = 500 – 510 m, 8 = 1000 – 1010 m, 9 = 2000 – 2010 m, 10 = 5000 – 5010 m).

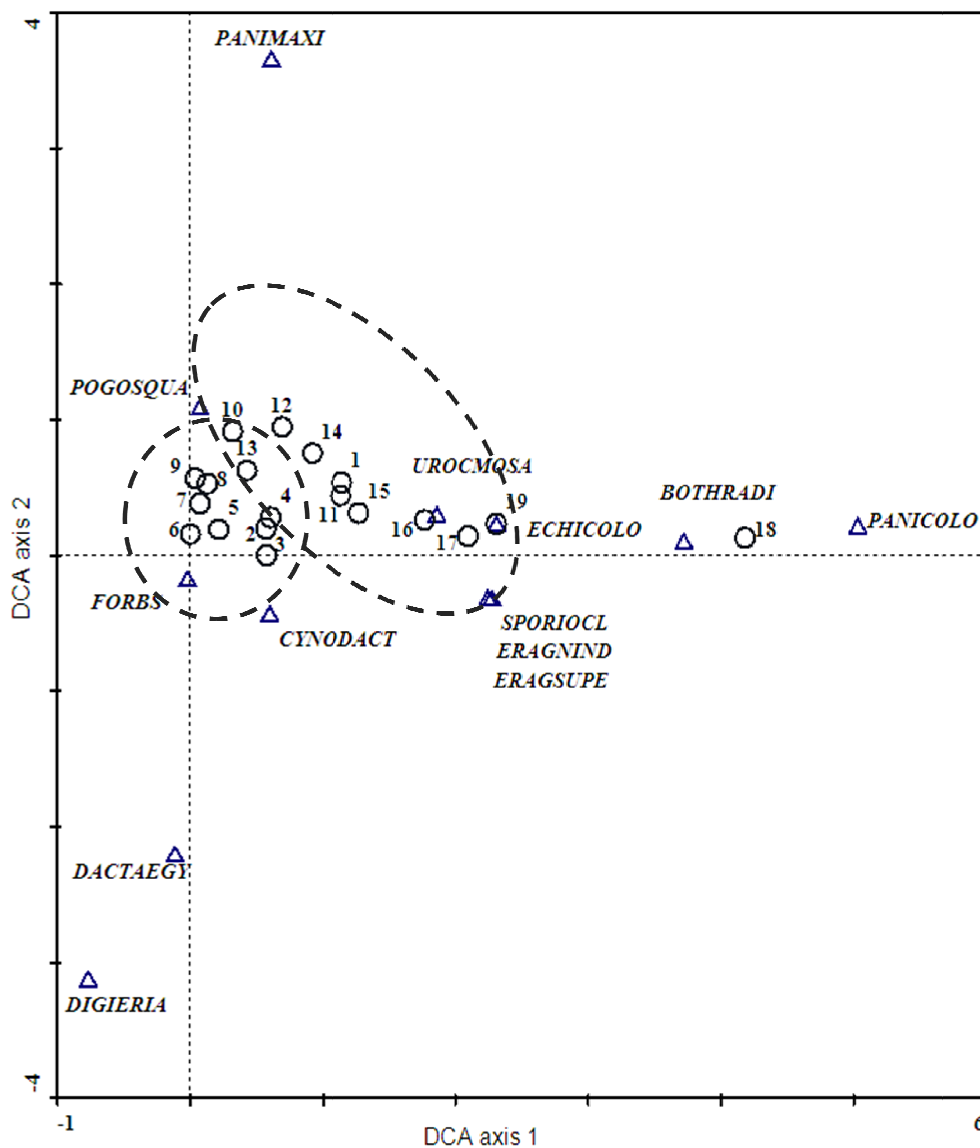


Fig. 3.2. First and second axes of a detrended correspondence analysis (DCA) of herbaceous species composition data along a distance-from-water gradient at Marheya waterhole (2006). The eigenvalues for DC axes 1 and 2 account were 0.823 and 0.093, respectively. The two axes together accounted for 52.6 % of the variation in species composition. Species abbreviations are tabulated (Table 3.2) in Appendix A. Circles represent sites; triangles represent species. Sites with small numbers are close to the waterhole, those with larger numbers are further from the waterhole (1 = 1 – 10 m, 2 = 10 - 20 m, 3 = 20 – 30 m, 4 = 30 – 40 m, 5 = 50 – 60 m, 6 = 60 – 70 m, 7 = 500 – 510 m, 8 = 1000 – 1010 m, 9 = 2000 – 2010 m, 10 = 5000 – 5010 m).

Distance from water had a significant effect on species composition (from CCA) at all sites (range in F: 3.004 to 8.842, range in p: 0.002 to 0.032), and effect of time and the interaction of distance with time were also significant at all sites (range in p: 0.002 to 0.054). This result was confirmed by the blocked MRPP (Table 3.1, Appendix A), for which the T-statistic (a measure of the difference between two groups) was significant (range in p: 0.00003 to 0.02538) for all sites, although a large range was obtained (Range in T: -2.47 to -10.60). Larger compositional changes occurred between 1990 and 2006 at open sites (mean T = -7.17) than at closed sites (mean T = -5.66).

All three closed sites became more homogenous in species composition (mean within-block ED) between 1990 and 2006, with a mean decline of 5.89 ± 4.20 in ED (measure of internal heterogeneity at a site). Four open sites gained heterogeneity, and two became more homogenous between 1990 and 2006. Sites that were open in 2006 were more heterogeneous in species composition than sites that were closed, in both 1990 (when all sites were open) and 2006 (Table 3.1, Appendix A). Thus, heterogeneity was related more to site (waterhole location) than to waterhole status *per se*. The patterns of change (where along the distance gradient compositional change occurred) along the piosphere gradients (ED between transects/plots at a site) were highly site-specific – there was no consistent response to distance from water.

At six sites, forbs declined in their relative contributions to species composition from 1990 to 2006, whilst increaser species (pioneer and sub-climax grass species that increase in abundance in heavily/overgrazed savanna or grassland, called Increaser II species by (Dyksterhuis 1949)) increased and decreasers (palatable climax grass species that decrease in abundance in over- or under-grazed grassland) declined (Fig. 3.3). The plot shown (Fig. 3.3) is from the Witpens waterhole, selected because it is representative of this general pattern. Most sites experienced a large, significant overall increase in the relative abundance of *Urochloa mosambicensis* (range in t: 1.479 to 7.213, range in p: 0.001 to 0.021). Changes in this species were the foundation for changes in the increaser II group described above. Other important species in this functional group where *Dactyloctenium aegyptium*, *Eragrostis trichophora* and *E. superba*, which increased at most sites from 1990 to 2006. Temporal changes to the decreaser group were mostly determined by changes in *Digitaria eriantha*, *Themeda triandra*, *Panicum coloratum* and *Brachiaria nigropedata*.

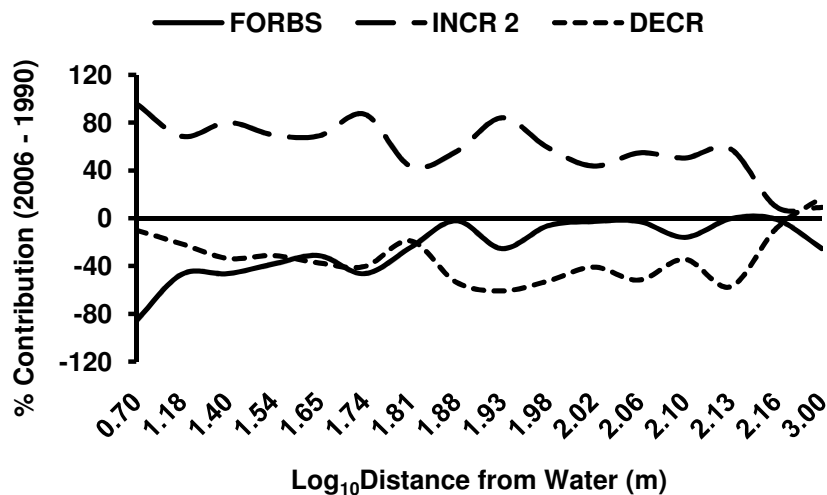


Fig. 3.3. The change in the contribution (%) of different plant functional groups between 1990 and 2006 (at the Witpens waterhole). Values > 0 indicate a relative gain in a particular plant functional group between 1990 and 2006; values < 0 indicate a loss.

There were generally large increases in the proportion of plot-pairs with low (< 0.25) Bray-Curtis dissimilarity values, from 1990 to 2006. These losses of compositional heterogeneity were largely accounted for by plots close to the waterholes (0 – 150 m). There were, however, also increases in the proportions of plot-pairs with high (> 0.75) Bray-Curtis dissimilarity values, accounted for by comparisons of plots distant (> 500 m) from water with those close to water (< 150 m). Thus, between 1990 and 2006, there was a loss of compositional heterogeneity close to the waterholes, but areas close to water and areas distant from water diverged. Plots further than 500 m from water also tended to have high Bray-Curtis values when compared with each other. Thus, compositional heterogeneity increased as distance from water increased. There were no consistent patterns at closed or open waterholes with respect to compositional heterogeneity.

There were no distinct patterns in species richness and diversity associated with open or closed sites, and the responses of both indices to distance from water were highly variable, across sites and time periods. Four sites had an increase in Shannon's diversity from 1990 to 2006, and five sites stayed the same or decreased. This trend was mirrored by the equitability values. There was thus no clear piosphere pattern with respect to species diversity.

Basal cover & biomass (herbaceous)

Herbaceous biomass and basal cover both responded very variably to distance from water in 2006. In 1990, both basal cover and biomass were lowest in 20 – 100 m ‘sacrifice’ zones close to the waterholes and increased with distance from water beyond that, creating three-zoned piospheres. There were no significant differences in herbaceous basal cover between open and closed sites in 2006 ($t = 1.10$, $df = 8.12$, $p = 0.30$) nor between the same site groups in 1990 ($t = 0.14$, $df = 6.62$, $p = 0.89$), but there were significant increases in basal cover from 1990 to 2006 ($mean_{1990} = 0.77 \pm 1.09 \%$, $mean_{2006} = 8.57 \pm 6.46 \%$, $t = 12.369$, $df = 100$, $p < 0.001$). We note that mean annual rainfall in 1990 (MAP 501 mm) was lower than in 2006 (MAP 635 mm), which may have caused the higher basal cover in 2006 (Fig. 3.4). Herbaceous standing crop was also not significantly different between open and closed sites in 2006 ($t = 1.01$, $df = 6.00$, $p = 0.35$), nor between the same two groups of sites in 1990, when all waterholes were open ($t = 0.10$, $df = 2.59$, $p = 0.92$). Herbaceous standing crop was higher also significantly higher ($t = 13.131$, $df = 68$, $p < 0.001$) in 2006 ($mean = 4\,746.47 \text{ kg}\cdot\text{ha}^{-1}$) than in 1990 ($mean = 957.22 \text{ kg}\cdot\text{ha}^{-1}$).

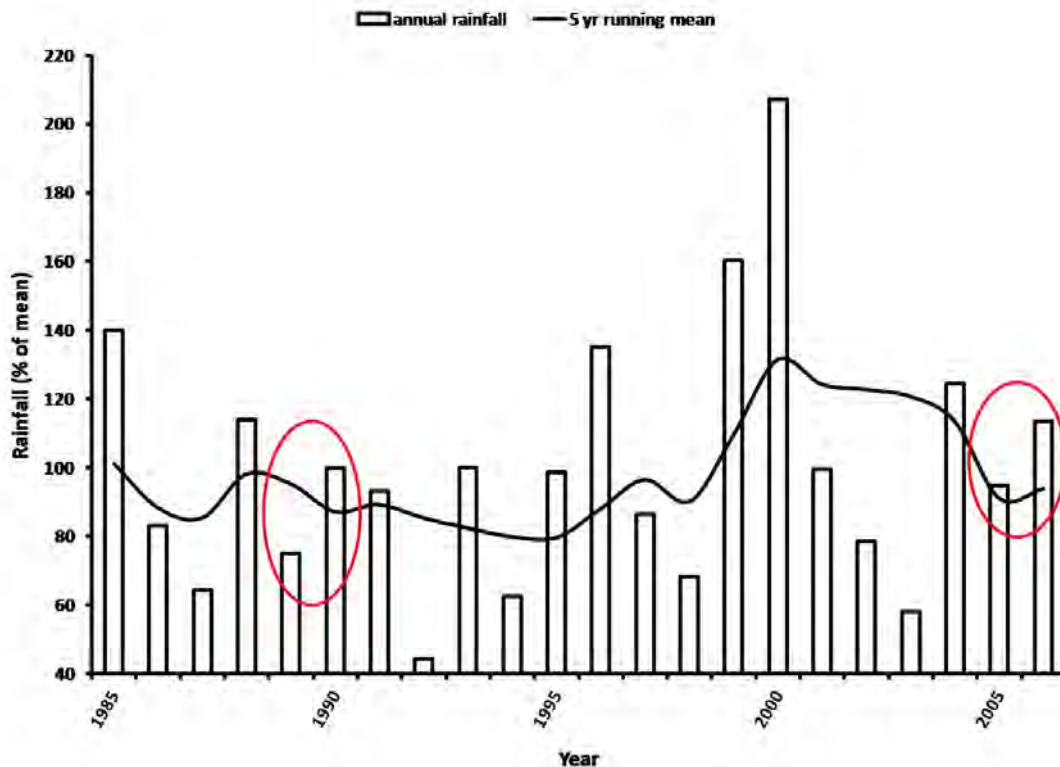


Fig. 3.4. The change in annual wet season (July – June) rainfall (solid line) and five-year running mean rainfall (dashed line), as a % of the long-term average, between 1985 and 2006. The two study periods (1989-1990 and 2005-2006) are indicated by circles.

Woody composition and structure

We found no significant effect of waterhole closure on overall woody plant density, nor for any specific tree height class (range in t : 0.38 to 1.27, range in df : 4.35 to 6.93, range in p : 0.26 to 0.80). In addition, there were no consistent patterns along the distance from water gradient for any tree height class.

At most sites, 20 – 40 % of the comparisons between distance classes yielded low Bray-Curtis dissimilarity values (< 0.25) for woody community structure, but all 11 sites also had at least 20 % of comparisons with high Bray-Curtis values (> 0.75). Thus, there was an almost binomial pattern in heterogeneity – almost half the comparisons between distance classes at each site had very low heterogeneity, and the remainder very high heterogeneity. Unlike the comparisons made for herbaceous species composition, there were no piosphere patterns for

heterogeneity – transects with particular tree height distributions occurred along the entire distance gradient.

Distance from water did not have a significant effect ($p > 0.1$) on woody community composition at the majority of sites ($n = 8$). The only species for which a general trend was noticeable was *Dichrostachys cinerea*. This species was most abundant at intermediate distances (200 – 500 m) from water.

The analysis of species compositional dissimilarity between all pairs of transects at each piosphere revealed that six sites did not have any pairs with Bray-Curtis values below the homogeneity threshold value of 0.25, and of the remaining five sites, only three had more than 10 % of pairs below this threshold. For the heterogeneity threshold value (Bray-Curtis > 0.75), only two sites had less than 50 % of pairs that exceeded the threshold. Three sites had more than 80 % of pairs with Bray-Curtis values of more than 0.75. Therefore, overall, there was high compositional heterogeneity in the woody community at the waterholes surveyed. Shannon's diversity (H') showed no distinct piosphere pattern at open sites (constant diversity along gradient), although diversity increased with distance at three closed sites. Equitability (J) followed a similar trend to diversity (H') along the distance gradient at most sites.

3.4 DISCUSSION

This study was undertaken to shed light on the process of piosphere progression in sub-humid savanna in the KNP. The study was a follow-on from an earlier piosphere study conducted in 1990 (Thrash 1993), and the broad objective was to quantify spatio-temporal changes to herbaceous vegetation composition and structure around the same artificial waterholes described by Thrash (1993), taking waterhole status (open versus closed). Since Thrash's (1993) study was completed, the water provision policy in the KNP has changed and a large number of waterholes have been closed since the mid-1990s. Of the waterholes surveyed by Thrash (1993), approximately half remain open; the others are closed. We thus tested the hypothesis that those vegetation indicators such as plant species composition, biomass and basal cover would show recovery around closed waterholes, and that piospheres around open waterholes will have expanded since 1990. Our findings that herbaceous biomass and basal cover increased significantly all at waterholes, regardless of status, and that there were clear piosphere patterns at neither open nor closed waterholes in 2006, in contrast to 1990, suggest that

waterhole closure cannot be explicitly linked to vegetation “recovery”, as we hypothesized. There was no distinction between open and closed waterholes for herbaceous basal cover and biomass, and open waterholes have not shown piosphere expansion since 1990, as we predicted. Herbaceous species composition, however, did respond significantly to distance from water, time and their interaction, at all sites. We found clear piosphere patterns in both 1990 and 2006 at most sites, and if the increase in disturbance-tolerant, increaser grass species at most sites, along with the concomitant decrease in grazing-sensitive decreaser species, can be construed as evidence for piosphere degradation, then our hypothesis that piospheres around active sites would expand between 1990 and 2006 was met. The loss of the outermost piosphere zone between 1990 and 2006 supports piosphere expansion with respect to herbaceous composition. We also hypothesized that there could be piosphere recovery at closed sites, however, and this hypothesis is rejected for herbaceous species composition, because no significant increases in climax, grazing-sensitive species were recorded at closed waterholes. However, we did record greater compositional changes (i.e. greater gains in the relative abundances of increaser grass species) at open sites than at closed sites, indicating that waterhole status is an important determinant of herbaceous species composition. Although we did not directly measure herbivore activity around open and closed waterholes, this relatively higher increase in the abundance of grazing-tolerant increaser grasses at open sites suggests that closed waterholes are experiencing lower herbivore activity.

Urochloa mosambicensis was the most abundant increaser II species found in this study. It was common in 2006, but absent in 1990. This species is unusual among increaser II grasses, because although it increases in abundance following heavy grazing, it is palatable and has a high grazing value (Van Oudtshoorn 2002). The high relative abundance of *U. mosambicensis* at all waterholes in 2006 is thus not of concern from a forage production perspective. However, some sites had almost monospecific stands of this species (up to 98 % in some cases), accounting for the loss of compositional heterogeneity between 1990 and 2006. This change in the abundance of *U. mosambicensis* in the KNP in general may be in response to short-term climatic perturbations or a longer-term response to grazing intensity. Kennedy *et al.* (2003) reported a large-scale increase in *U. mosambicensis* following the 1991 – 1993 drought in the KNP, which persisted until 1997. Above-average rainfall was recorded in the KNP between 2000 and 2006 (Figure 3.4), but we found no reversal of the trend reported by Kennedy *et al.* (2003).

The higher rainfall recorded in 2005-2006, compared to 1989-1990, accounts for the high herbaceous biomass and basal cover recorded in the current study, compared to that recorded in 1990 (Thrash 1993). Perennial vegetation cover is related to ecosystem function (Holm & Friedel 2002). Vegetated patches in an ecosystem capture the resources (water, nutrients, soil, organic matter and seeds) lost by bare patches as run-off water moves over the landscape (Tongway & Ludwig 2003a; b; Tongway & Hindley 2004; Ludwig *et al.* 2007). Losses of basal cover often indicate that an ecosystem is losing functionality (Briske *et al.* 2006). The ability of an ecosystem to respond to rainfall inputs by producing biomass and increasing perennial vegetation cover is a good indicator of resilience. The positive responses of these two functional vegetation attributes (biomass and basal cover) to above-average rainfall in the 2005-2006 growing season suggest that long-term artificial water provision in the KNP has not seriously affected ecosystem resilience. In addition, the strong piosphere zonation for basal cover and biomass in 1990 (Thrash 1993), compared to the absence of clear piospheres in 2006, indicate that piospheres in the KNP are intermittent. The lack of a waterhole closure effect, coupled with such piosphere intermittency for these two indicators, suggests that climate may have a more important effect on ecosystem function than herbivore utilization in the KNP. However, the response of herbaceous species composition to distance from water suggests that herbivores have an important effect on the herbaceous community. Other studies have also shown that herbivores may have a long-term, cumulative effect on vegetation composition, but that biomass and total plant basal cover respond more strongly to rainfall variability (O'Connor 1994; O'Connor & Roux 1995; Fuhlendorf *et al.* 2001).

Piosphere intermittency in the KNP may also be linked to the low herbivore density. The KNP has a average herbivore biomass of only 1 750 - 2120 kg.km⁻² (East 1984; Mills & Funston 2003), compared to more than 20 000 kg.km⁻² in the Serengeti ecosystem (Mills & Funston 2003) during the wet season, 7337 kg.km⁻² in Hluhluwe-Umfolozi Park (East 1984) and 2000 – 10 000 kg.km⁻² in the private game reserves adjacent to the KNP (personal communication from Peel, M. 2009).

The lack of a waterhole closure effect on herbaceous species composition in this study raises two possibilities. Firstly, herbivore utilization around closed waterholes may not have changed after waterhole closure. Waterhole density was historically high in the KNP (Gaylard *et al.* 2003), and even though a large number of waterholes have been closed since the mid-1990s,

waterhole density remains high. Most regions of the KNP are accessible to water-dependent herbivores. Thus, waterhole closure may not yet have created extensive grazing refugia in the park. In addition, herbivores may still be strongly attracted to closed waterholes for the productive forage available in short-grass patches and grazing lawns that developed after frequent grazing during the waterholes' active periods (van der Schijff 1959; Thrash 1993). The alternative scenario is that herbivore utilization has decreased following waterhole closure, but species composition has not recovered (i.e. the abundance of palatable, grazing-sensitive, climax species has not increased). This would suggest that a slowly reversible or even irreversible compositional threshold has been crossed because of artificial waterhole provision in the park. Long-term (30 – 80 years) trampling, nutrient deposition and heavy grazing around artificial waterpoints in the KNP may have pushed the ecosystem into an alternative stable state (dominated by pioneer and sub-climax herbaceous species) requiring a major perturbation (i.e. above and beyond waterhole closure) to return it to its initial state, if the initial state is assumed to be one characterized by palatable, grazing-sensitive, climax species. Longer-term piosphere monitoring is required to separate these two hypothesized explanations for the lack of a waterhole closure effect.

In contrast to what we report for the herbaceous community, no piosphere patterns were found in the woody community in this study – either compositionally or structurally. Browsers appear not to have an effect on the woody community. Browsers are less water-dependent than grazers are, because their forage generally has a higher water content (Young 1970; Western 1975; Clegg 1999). Thus, browsing pressure is not concentrated around artificial waterholes, explaining the lack of piosphere patterns for community composition or structure. Other studies have also suggested that high levels of elephant impact and regular, high-intensity fires in the KNP may have homogenized the woody community at a landscape scale (Eckhardt *et al.* 2000; Scholes *et al.* 2003). Such homogenization may also influence the lack of clear piosphere patterns - although the high proportion of Bray-Curtis values above 0.75 (for composition and structure) found in our study seem to contradict this, at least at the finer grazing-gradient scale.

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3.6 APPENDIX A

Table 3.1: The A (MRPP statistics), T and p values from the blocked MRPP tests for each site, mean within-group heterogeneity (Euclidean distance) for 1990 and 2006, and p values of the test (ANOVA) for significant differences between the mean with-in group heterogeneity for 1990 and 2006.

<i>Site</i>	<i>T</i>	<i>p (MRPP)</i>	<i>A</i>	<i>Mean</i> <i>1990</i>	<i>Mean</i> <i>2006</i>	<i>F</i>	<i>p (heterogeneity)</i>
Capricorn	- 6.852	0.00055	0.453	49.595	40.967	1.747	0.1972
Marhumbeni	-3.7080	0.00723	0.274	13.574	12.529	0.202	0.6342
Marheya	-6.4228	0.00082	0.417	42.656	34.674	0.728	0.3659
MEAN (Closed)	-5.661		0.381	35.275	29.39		-
Manzimhlope	-3.951	0.00584	0.310	51.565	30.417	6.555	0.0165
Mananga	-10.597	0.00001	0.301	50.061	61.740	3.480	0.0693
Shivulani	-2.4695	0.02538	0.225	43.026	67.960	3.579	0.0797
Tihongonyeni	-9.8014	0.00006	0.576	58.844	15.061	17.116	0.0002
Timbiteni	-6.4744	0.00036	0.238	46.183	48.709	0.192	0.6710
Witpens	-9.690	0.00003	0.2879	46.341	55.676	2.052	0.1618
MEAN (Open)	-7.1639		0.3256	49.3367	46.5938		

Table 3.2: Species abbreviations for DCA ordination biplots.

<i>Species code</i>	<i>Name</i>
BOTHRADI	<i>Bothriochloa radicans</i>
BRACNIGR	<i>Brachiaria nigropedata</i>
CHLOVIRG	<i>Chloris virgata</i>
CYNODACT	<i>Cynodon dactylon</i>
DACTAEGY	<i>Dactyloctenium aegyptium</i>
DIGIERIA	<i>Digitaria eriantha</i>
ECHICOLO	<i>Echinochloa colona</i>
ERAGCILI	<i>Eragrostis cilianensis</i>
ERAGNIND	<i>Eragrostis nindensis</i>
ERAGSUPE	<i>Eragrostis superba</i>
ERAGTRIC	<i>Eragrostis trichophora</i>
<i>Forbs</i>	Flowering herbs
PANICOLO	<i>Panicum coloratum</i>
PANIMAXI	<i>Panicum maximum</i>
POGOSQUA	<i>Pogonarthria squarrosa</i>
SCHMPAPP	<i>Schmidtia pappophoroides</i>
SPORIOCL	<i>Sporobolus ioclados</i>
THEMTRIA	<i>Themeda triandra</i>
TRAGBERT	<i>Tragus berteronianus</i>
UROCMOSA	<i>Urochloa mosambicensis</i>

CHAPTER 4: SOIL PHYSICAL AND CHEMICAL GRADIENTS AROUND ARTIFICIAL WATERHOLES IN THE KRUGER NATIONAL PARK

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Soil gradients in piospheres

Abstract There is increasing emphasis in protected area management on the conservation of ecosystem resilience and heterogeneity. Rangeland degradation includes detrimental changes to the soil and vegetation complex, and losses of ecosystem heterogeneity and resilience. Changes to the soil that result from management interventions such as artificial water provision are of critical importance. This study addressed the spatio-temporal patterns of soil properties (texture, infiltration capacity, compaction, total nitrogen, total phosphorus, organic matter and pH) along 5 km distance-from-water gradients within piosphere systems in the Kruger National Park, against a backdrop of waterhole closure. Results indicated no consistent effect of water provision on these variables and spatial distributions of most measured soil properties at 11 study sites. Only soil pH and soil compaction responded consistently to distance from water, both declining along the piosphere gradient, as predicted by the conventional piosphere model. Waterhole closure had no significant effect on the response patterns of soil properties to distance-from-water. We concluded that there have been no significant soil changes in response to water provision. Vegetation recovery after waterhole closure should not be limited by soil chemistry or soil physical properties. The soil patterns we detected are a reflection of underlying abiotic heterogeneity and do not appear to be strongly linked to the spatial distribution of herbivore impact.

Key words: soil fertility; ecosystem thresholds; rangeland recovery; resilience; degradation; herbivore-soil interactions

4.1 INTRODUCTION

The term 'piosphere' (Lange 1969) refers to the phenomenon in which the foraging area available to herbivores decreases exponentially with distance from water (Lange 1969; Derry 2004), creating herbivore utilisation gradients in a range of soil and vegetation parameters (James *et al.* 1999; Heshmatti *et al.* 2002; Landsberg *et al.* 2003; Smet & Ward 2005; 2006). Piospheres are important because they affect landscape-scale patterns of heterogeneity and resilience (Gaylard *et al.* 2003; Derry 2004).

Monitoring soil responses to rangeland disturbance is important, because the soil is an important indicator of degradation (Smet & Ward 2006). Soils, particularly in arid and semi-arid rangelands, are said to have lower resilience to disturbance than vegetation (Thomas 1993). Unless vegetation changes are accompanied by soil degradation, ecosystem resilience may not be unduly compromised (Clegg 1999). On resilient soils, vegetation changes may occur without the soil reflecting the new state. Typically, compositional and structural vegetation changes in response to a disturbance are reflected by altered soil water infiltration rates and patterns of nutrient availability (Abel & Blaikie 1989; Doughill & Cox 1995). The state of the vegetation in most ecosystems is at least as dependent on climatic conditions as it is on herbivore population dynamics (Behnke & Scoones 1993). Recording vegetation composition at any one time provides only a snapshot of what is happening in the system in the short term (Smet & Ward 2006), and does not necessarily indicate long-term vegetation trends. For this reason, soil indicators may provide a better picture of rangeland condition, because they are less affected by short-term climatic fluctuations (Smet & Ward 2006) and because once soil resilience is lost, the system as a whole may be rendered unstable (Thomas 1993).

Tolsma *et al.* (1987) identified two soil processes associated with artificial waterholes in savanna systems. Herbivores transport nutrients (via dung and urine) from the surrounding savanna, centripetally towards the waterhole. Trampling and hoof action by herbivores also leads to compaction and loss of water-infiltration capacity near waterholes. The severity of trampling is directly proportional to the biomass of herbivores utilising the waterhole. Trampling is the primary agent responsible for physical soil changes. The concentration of herbivore pressure into increasingly smaller areas with declining distance from water (Derry 2004) results in a trampling gradient inversely proportional to distance from water. A range of associated soil properties corresponds closely to the severity of trampling and exhibit the following typical gradients: soil

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compaction and soil water infiltration rate (Kelly & Walker 1976; Andrew & Lange 1986; Perkins & Thomas 1993; Thrash 1993), game path coverage and intensity (Lange 1969; Andrew & Lange 1986) and changes in soil texture (Lange 1969; O'Connor 1985; Andrew & Lange 1986; Pandey & Singh 1991; Thrash 1993).

The severe trampling in piospheres in savannas is linked to losses of vegetative cover (Thrash 1993) and loss of soil structure (Strang 1974; O'Connor 1985; Thrash 1993). These processes in turn contribute to accelerated water erosion, particularly when acting in combination with soil capping and losses of infiltration capacity. Soil textural changes occur because the loss of the finer fractions of the soil (clay, silt, fine sand) occurs faster than the loss of coarser sand particles, and has been attributed to severe trampling (Strang 1974; O'Connor 1985).

This study examined the spatio-temporal patterns of soil physical (compaction, infiltration and particle size distribution) and chemical (pH, N, P, organic matter) properties in active (waterhole open) and recovering (waterhole closed) piosphere systems in the Kruger National Park (KNP). Recent (1999/2000) waterhole closure in the KNP provides an ideal opportunity to study the resilience of soil characteristics in piosphere systems.

Our predictions for this study were:

1. Soil pH, organic matter and total soil nitrogen and phosphorus would decline with distance from water, because soil nutrients accumulate close to waterholes due to dung and urine deposition by herbivores.
2. Soil compaction would decline with distance from water, because heavy trampling by herbivores concentrating close to the waterhole will result in high compaction soils in that area.
3. Soil water infiltration rate would increase with distance-from water, because the compacted soils near the waterhole impede infiltration.
4. Soil water infiltration rate will be lower in 2006 than 1990, because piospheres become more severe as they age (Adler & Hall 2005).
5. Piospheres around open waterholes will have higher soil pH, N, P and organic matter than those around closed waterholes, because the open waterholes have provided drinking water for game during the six-year recovery period of the closed waterholes. Likewise, infiltration will be lower and compaction higher around open waterholes than around closed waterholes.

4.2 METHODS

Study sites

Sites in the Kruger National Park at which vegetation and soil variables were sampled in 1990 by Thrash (1993) were resurveyed by us between April and June 2006 (Fig. 2.1). These sites include both closed and open waterholes (Table 4.1), and are representative of the four major land systems in the KNP: the Skukuza, Satara, Phalaborwa and Letaba systems (Venter 1990).

The Satara and Letaba land systems are characterised by clayey soils derived from the weathering of basic igneous rock (basalt). The Satara land system consists of fine-leaved tree savanna dominated by *Acacia nigrescens*, *Dichrostachys cinerea* and *Sclerocarya birrea* (Venter *et al.* 2003). The Letaba system is associated with *Colophospermum mopane* shrubveld, although *Combretum imberbe* is also abundant. The Satara land system receives higher rainfall than the Letaba system, and is thus characterised by higher perennial grass cover (Venter *et al.* 2003).

The Skukuza and Phalaborwa land systems are underlain by granitic rocks and have characteristic catenal gradients of soil type (Venter 1990; Venter *et al.* 2003). In the Skukuza land system, the vegetation of the sandy uplands included dense sands of deciduous *Combretum* spp. and *Terminalia* spp. The foot-slopes, where duplex soils are common, are characterised by more open, small-leaved, thorny shrub, in which several species of *Acacia* and *Albizia* occur along with *Dichrostachys cinerea*, *Euclea* spp., and *Combretum hereroense* (Venter *et al.* 2003). Grasses abundant on the foot-slopes tend to be nutritious bulk-growers. Seeplines are dominated by *Terminalia sericea* and *Combretum zeyheri*, and water-loving sedges and grasses such as *Eragrostis gummiflua*. Grass cover in the land system as a whole tends to be sparse, especially in dry years, but may be moderate to dense in wet periods.

The Phalaborwa land system is characterised by *Combretum apiculatum* and *Colophospermum mopane* bushveld (Venter *et al.* 2003). *C. apiculatum* typically occurs on the shallow gravels and sandy soils on the crests, whereas *C. mopane* grows in the clayey soils of the footslopes (duplex soils) and along dolerite dykes.

At each waterhole, a single belt transect 5 m wide was laid out along a gradient extending from the edge of the waterhole to 5 000 m from the waterhole, from within which all measurements were taken.

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Table 4.1. The dates (month and year) of opening and closure of the eleven artificial waterholes surveyed in 2006, with current status given

Land type	Site	Current status	Date opened	Date closed
Skukuza	Manzimhlope	Open	01/1933	
	Timbiteni	Open	01/1962	
	Shiteve-teve	Open	05/1973	
Satara	Witpens	Open	unknown	
	Mananga	Open	07/1973	
	Marheya	Closed	07/1962	Structure removed 2001
Phalaborwa	Shivulani	Open	01/1935	
	Marhumbeni	Closed	07/1970	Structure removed 2001
	Wik-en-Weeg	Closed	1973	Unknown (assumed 2001)
Letaba	Capricorn	Closed	02/1975	Original structure removed 2001, roan enclosure completed 2002. Waterhole reopened 2002.
	Tihongonyeni	Open	04/1962	

Field data collection

Soil samples were collected at the following fixed distances from water, within the main 5 by 5000 m transect at each waterhole: 0 – 10 m, 40 – 50 m, 80 – 90 m, 110 – 120 m, 140 – 150 m, 500 – 510 m, 1 000 – 1 010 m, 2 000 – 2 010m and 5 000 – 5 010 m. At each distance, three soil cores were taken to a depth of 10 cm, using a soil auger. The three soil cores from each distance class were combined, and the following parameters were analyzed: the relative contributions of clay, silt and sand to soil texture, total soil nitrogen (N), available phosphorus (P), organic matter, and soil pH_{KCl}.

Soil water infiltration rate was measured using a Decagon mini disk infiltrometer (Decagon Devices 2005), at the following distances from water: 0 – 25, 50 – 100, 150 – 200, 500 - 550, 1000 - 1050, 2000 - 2050 and 5 000 - 5050 m. Within each distance class, the infiltration rate was measured three times. Readings were taken at 15 s intervals for 5 min, with a starting

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volume of 90 ml. We calculated the slope of the curve of cumulative infiltration and the square-root of time (C_1), and used this value in the following equation, to calculate the hydraulic conductivity of the soil:

$$k = C_1/A,$$

where k is hydraulic conductivity and A is calculated from the van Genuchten parameter of a particular soil type and the suction rate and radius of the infiltrometer disk. The van Genuchten parameter is a water retention index related to soil texture (van Genuchten 1980; Carsel & Parrish 1988; Decagon Devices 2005). Thrash (1993) measured soil water infiltration in 1990, at the same waterholes sampled in 2006 (excluding Shiteve-teve, Marheya and Wik-en-Weeg), also using a disk infiltrometer.

Soil compaction readings were taken with a dynamic cone impact soil penetrometer (Herrick & Jones 2002) at 10 m intervals between 0 and 100 m from the waterhole, and at 150, 200, 300, 400, 500, 1000, 2000 and 5000 m. Three measurements were taken at each distance, one in the centre of the 5 m belt and 1 m away on either side. For each reading, a hammer of 2 kg was dropped 40 cm distance for 5 strikes, and the distance that the shaft of the penetrometer dropped below the surface of the soil was recorded for each strike. Soil resistance to penetration (R_s), a measurement of compaction, was calculated as follows:

$$R_s = W_s/P_d,$$

where W_s is the work done by the soil and P_d the distance moved through the soil profile by the penetrometer. The work done by the soil in resisting penetration is calculated based on the amount of kinetic energy transferred from the hammer of the penetrometer to the cone with each strike (Herrick & Jones 2002). Soil resistance is measured in $J.m^{-1}$.

Data analysis

We fitted generalized additive models (GAMs) to describe the relation between distance from water and each soil variable. Generalized additive models (GAMs) were used to describe the functional relationship between soil variables and distance-from-water for each site (ter Braak & Smilauer 1997). For infiltration rate, GAMs were fitted for both periods (1990 and 2006). GAMs (Hastie & Tibshirani 1990) incorporate properties of generalized linear models (GLMs) and additive models (Quinn & Keough 2002). Each predictor is a non-parametric smoothing function, and scatterplot smoothers such as Lowess or cubic splines are used to

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obtain smooth generalizations of the relationship between predictor and response variables (Hastie & Tibshirani 1990; Quinn & Keough 2002). Various distributions for the dependent variable are allowed, and different functions can be used to link the expected values of the dependent variable and the values of the predictor variable. We specified a normal distribution and used an identity link function. Models with up to three smoothing functions were considered, and Akaike Information Criteria (AIC) were used to select the best-fit model (Akaike 1973; Buckland *et al.* 1993; Anderson & Burnham 2000). Variables surveyed in 1990 and reported in Thrash (1993) were re-analyzed for consistency with the current study.

We compared open and closed sites for all variables by calculating the area under the curve (AUC) for each site. Because GAMs could not be fitted to all sites for each variable, AUC was calculated from a scatter plot of the data (i.e. not using the fitted models). The AUC represented a single, integrated value for each site, and open and closed waterholes were compared using a t-test (equal variances not assumed) for each variable. For infiltration rate, also sampled in 1990, comparisons between the two time periods were made using paired-sample t-tests. For each distance from water at each site, the value recorded in 1990 was compared to that recorded in 2006.

4.3 RESULTS

Infiltration

In 1990, clear three-zoned piospheres well described by the logistic regression equation were present around all eleven waterholes (Thrash 1993; 1997). In 2006, the responses of infiltration to distance from water were highly variable and no consistent piosphere pattern was found. Water infiltration rates in 2006 were significantly higher than in 1990 ($\text{mean}_{1990} = 0.0028 \pm 0.00018 \text{ cm.s}^{-1}$, $\text{mean}_{2006} = 0.0406 \pm 0.00808 \text{ cm.s}^{-1}$ $\text{df} = 164$, $t = -3.94$, $p \leq 0.001$), but there were no significant differences between open and closed waterholes in 2006 ($\text{mean}_{\text{open}} = 0.027 \pm 0.0063 \text{ cm.s}^{-1}$, $\text{mean}_{\text{closed}} = 0.065 \pm 0.0194 \text{ cm.s}^{-1}$, $\text{df} = 3.11$, $t = -1.40$, $p = 0.25$).

Soil compaction

We predicted that soil compaction would be highest close to the waterholes where animals concentrate. As predicted, most sites had a slow, approximately linear decline in soil resistance

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along the distance gradient (Fig. 4.1), and there were no significant ($p > 0.1$) differences in soil compaction between open and closed sites ($t = -1.11$, $df = 3.02$, $p = 0.35$).

Soil texture

There were also significant ($p \leq 0.001$) changes in the relative contributions of each soil particle size class (clay, silt and sand) to soil texture along distance from water gradients at most sites. However, these changes followed no consistent and predictable piosphere patterns, with maxima and minima occurring at various distances from water at the eleven study sites. There was also no significant effect of waterhole closure (range in t : 0.140 to 0.769, range in df : 6.93 to 8.99, range in p : 0.46 to 0.89) on soil textural patterns.

Very few significant relationships occurred between soil texture and the other physical and chemical soil variables measured in this study. Total soil nitrogen increased significantly with the percentage of both clay and silt in the soil, and declined significantly with the total sand content of the soil. Phosphorus and soil compaction did not vary significantly with any soil-particle size class. Soil organic matter increased linearly with the silt content of the soil, but had no clear relationships with clay or sand content. Soil pH peaked at intermediate clay and sand content.

Soil fertility indices

There was no consistent response to distance from water across the eleven study sites for total soil nitrogen, total soil phosphorus or organic matter. Soil pH was the only soil chemical variable to respond consistently along the distance gradient, with a negative linear response at most sites (Figure 4.2), as predicted. The response of soil pH to distance from water at the Shiteve-teve waterhole has been presented (Figure 4.2) as an example of the general response pattern found at the remaining ten sites. No significant ($p > 0.10$) changes occurred between open and closed sites for soil pH, organic matter, total soil nitrogen or total soil phosphorus (range in t : 0.14 to 0.26, range in df : 5.29 to 7.51, range in p : 0.80 to 0.89).

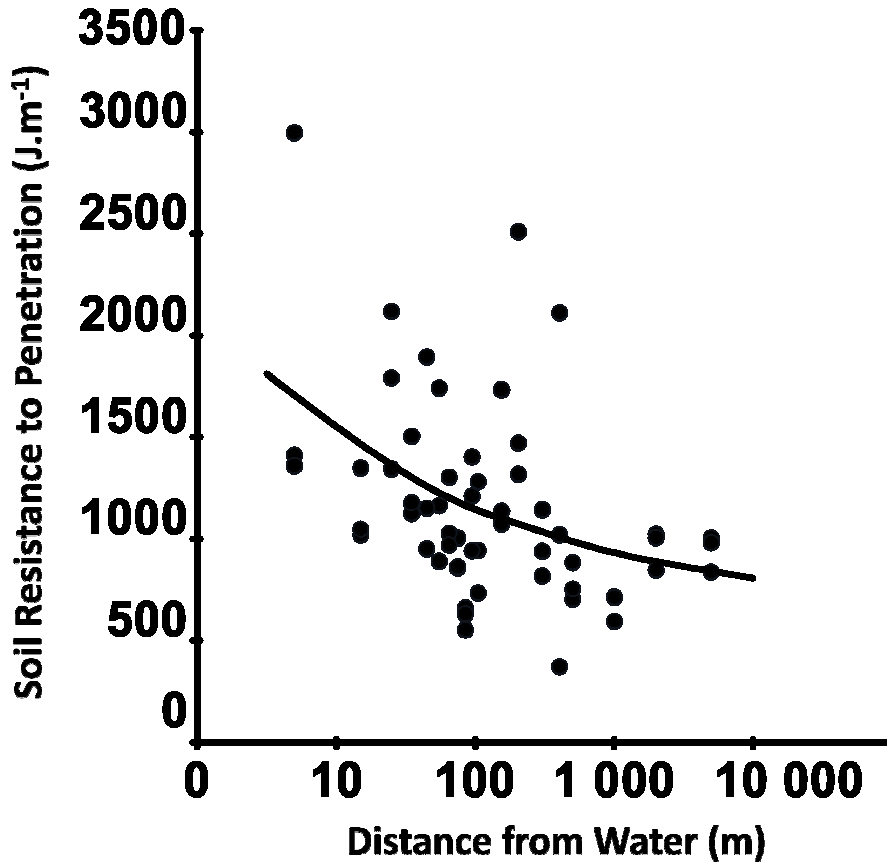


Fig. 4.1. The change in soil compaction, measured as resistance to penetration (J. m^{-1}), along the distance from water gradient at the Witpens waterhole. Observed values = solid dots, line = fitted GAM.

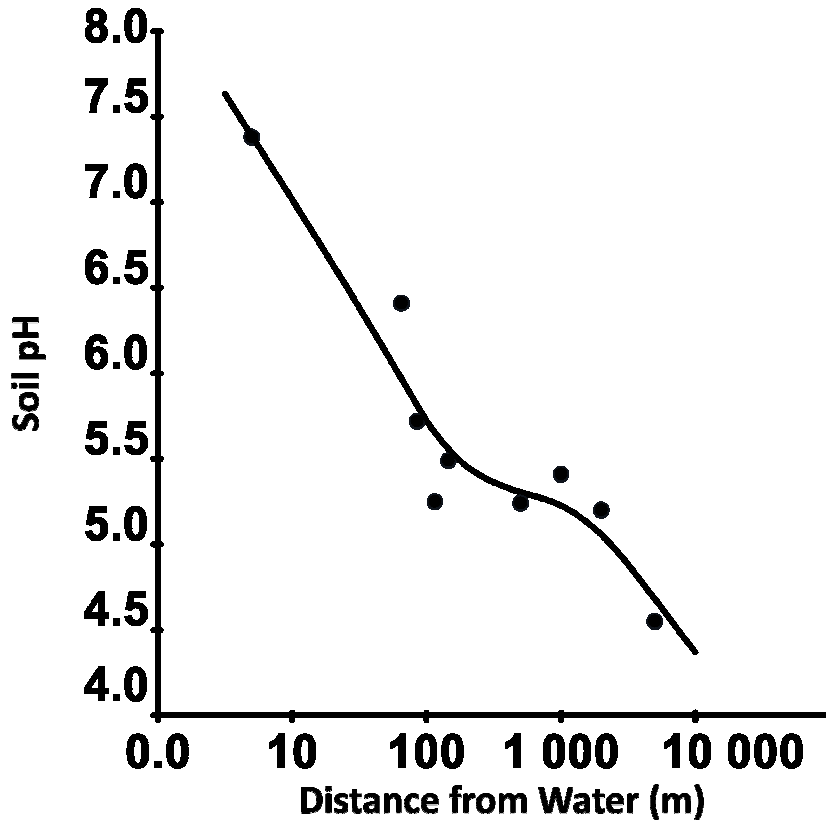


Fig. 4.2. The decline in soil pH along the distance from water gradient at the Shiteve-teve waterhole. Observed values = solid dots, line = fitted GAM.

4.4 DISCUSSION

Piosphere patterns

Smet and Ward (2006) examined a similar range of soil parameters to those in this study, along grazing gradients associated with active waterholes on communal and commercial rangelands in the Kalahari Thornveld (Acocks 1988). They found that soil pH values near the waterholes were high, and declined with distance-from-water up to 100m, after which an asymptote was reached. Soil resistance (the inverse of soil electrical conductivity and a measure of the concentration of ions in the soil, not the same as physical resistance to penetration as measured in this study) tended to be low near the waterhole, increasing with distance-from-water up to 100, after which no further changes occurred. Total soil nitrogen in communal livestock and commercial game ranching systems did not change significantly along the distance-from-water gradient. Likewise, clear piosphere gradients for total soil nitrogen did not emerge in the current study. In Smet and Ward's (1996) case, nitrogen levels in the commercial livestock

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system were high near the waterhole, declining to the levels recorded in the other two management systems at 75 m from the waterhole. Beyond that, no further changes occurred along the grazing gradient. Smet and Ward (2006) recorded similar patterns for available phosphorus (commercial livestock and game ranching systems) and soil organic carbon (commercial livestock system), with a negative linear response between 0 and 75 m from the waterhole, and no effect thereafter.

Other studies have recorded similar soil nutrient patterns along grazing gradients associated with waterholes (Tolsma *et al.* 1987; Doughill & Cox 1995; Stumpp *et al.* 2005; Gebremeskel & Pieterse 2006). These increases in soil nutrients around waterholes occur because herbivores import nutrients (deposited as dung or urine) from outlying areas of the rangeland (Tolsma *et al.* 1987). The high organic carbon, in particular, is related to dung deposition by herbivores that have removed plant material (through grazing) far from the water source, and transported it to the waterhole.

The distance-from-water gradients recorded for physical and chemical soil parameters in this study were highly site-specific. The ranges of soil physical and chemical properties and their patterns of change along the gradients differed between sites. Our results did not conform to our predictions for most variables. This variability makes it difficult to attribute the soil patterns we recorded directly to herbivore impact within the context of water provision. The soil gradients at our sites likely reflect underlying, naturally high spatial soil heterogeneity and plant-herbivore-soil feedbacks at this localised patch-scale, rather than at the piosphere-induced grazing-gradient scale. Average distance from water is low (< 5 km) in the KNP as a whole (Thrash 1993; Gaylard *et al.* 2003). The high waterhole density (Thrash 1993; Gaylard *et al.* 2003) and relatively low herbivore density in the KNP (East 1984; Mills & Funston 2003) disperses animal impact, and herbivore impacts on the soil will not necessarily correspond to distance from water, because this does not constrain herbivore foraging. The presence of predators in the KNP may also discourage herbivores from lingering close to waterholes, further reducing nutrient build-up close to water (Smuts 1978). If herbivores are not spending long periods near waterholes (and depositing significant amounts of dung and urine in the vicinity), then the patterns documented by Smet and Ward (2006), Tolsma (1987), and Dougill *et al.* (1995) are unlikely to emerge.

Soil pH was the only chemical variable in this study that responded consistently to distance from water – declining along the piosphere gradient, as predicted from previous studies.

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One possible explanation is that nutrient inputs to soil near waterholes from herbivore dung and urine increases the base status of the soil, increasing the pH of the soil in the centre of the piosphere. The ranges of pH values recorded in this study are within range for those reported for granitic (4.5 – 8) and basaltic (5 – 8) soils in the KNP (Venter *et al.* 2003). The response of soil pH to distance from water indicates that herbivore utilization of rangeland close to waterholes is impacting upon soil chemistry, but the failure of total soil nitrogen, total soil phosphorus and organic matter to conform to the piosphere model suggests that this may be minimal and not cause for management concern in the KNP. The waterholes that we surveyed in this study, both open and closed, have a 30 - 80 year history. The lack of clear soil chemical patterns around waterholes suggest that soil changes in this system accumulate very slowly, although the pH gradients recorded indicate that there is the potential for these gradients to develop over time.

Total soil N increased with the clay and silt content of the soil in this study, which suggests that changes in soil texture (that often indicate catenal changes) are more important than distance-from-water gradients in determining the levels of mobile elements such as nitrogen in the soil (Scholes & Walker 1993). This relationship to soil texture is explained by the positive correlation between the clay content of the soil and the water and solute-holding capacity of the soil (White 2006). Nitrogen and other mobile nutrients will leach out of sandy soils faster than clayey soils. The less mobile nutrients (e.g. P) in the soil were not related to soil texture in this study. These results also point to the role of the underlying abiotic template in the KNP in determining soil function, which appears to override herbivore impact on the soil along distance-from-water gradients. The relatively low herbivore biomass in the KNP (East 1984; Mills & Funston 2003) will also contribute to the slow accumulation of nutrients around artificial waterholes, resulting in the lack of clear piosphere patterns recorded in this study.

Resilience of Soil Properties

Smet and Ward's (2006) study of soil chemistry around artificial waterholes in the Kalahari indicated that soil nitrogen and organic carbon levels recover rapidly after herbivore utilization pressure is reduced. Within 10 years of a reduction in herbivore stocking pressure, soil nitrogen and organic carbon close to artificial waterholes were similar to levels in the rangeland in general (Smet & Ward 2006). This implies high resilience with respect to these two parameters – both of which are highly mobile. Soil phosphorus levels remained high after this

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reduction in stocking rates, implying that longer time periods are required before recovery can be detected for less mobile soil elements (Smet & Ward 2006). Phosphorus does not leach, volatilise or mineralize as rapidly as soil nitrogen or carbon (Whitehead 2000; Smet & Ward 2006). Our failure to detect strong piosphere patterns in this study, coupled with the large increases in infiltration rates between 1990 and 2006, suggests that soil resilience has not been affected by long-term artificial water provision in the KNP to a point where a 'change of state' precludes recovery in the long term. This bodes well for vegetation recovery around closed waterholes in future. We found clear negative, linear responses of soil compaction to distance from water, indicating that there is a significant effect of trampling by herbivores on soils close to waterholes. However, since this has not compromised infiltration capacity, this appears not to have had an effect on soil function.

For all the soil physical and chemical parameters we measured, active and recovering piospheres were not significantly different. Two possible scenarios emerge. Open sites are possibly not experiencing significantly more impact (in soil chemistry) than the rangeland in general, or closed sites have not experienced any change in herbivore impact following waterhole closure. The temporal scale at which soil changes occur may also account for this lack of a waterhole-status effect. Waterholes in this study have only been closed for seven years, although Smet and Ward (2006) recorded changes ten years after a management change in the Kalahari. It may also be true that long-term herbivore activity around waterholes in the KNP has caused the ecosystem to shift into an alternative stable state, which requires a large perturbation (larger than waterhole closure) to revert to its initial state (however that may be defined). In this instance, the time elapsed since waterhole closure is of no consequence in explaining changes (or a lack of change) in vegetation and soils.

The relative strength and importance of top-down and bottom-up controls of soil function in the KNP also need to be questioned - soil quality in this system may not be controlled by herbivore impact *per se*, but by broader-scale climatic and geomorphological dynamics. Herbivore impact does not appear to be sufficient to impose strong and ubiquitous piosphere patterns on the soil in this system, and soil resilience does not seem to have been lost because of water provision.

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**CHAPTER 5: VEGETATION PATCHINESS AND ECOSYSTEM
FUNCTION RESPOND TO ARTIFICIAL WATER PROVISION IN THE
KRUGER NATIONAL PARK**

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Abstract Vegetation patchiness is an important feature of grazed rangelands, because it has implications for ecosystem function and resilience, and heterogeneity and biodiversity conservation. We examined patch size, type and distribution and ecosystem function within piosphere systems in the Kruger National Park, to contribute to a broader understanding of the effect of artificial water provision on ecosystem function. Five patch indicators were sampled (total patch area, patch frequency, patch area index, landscape area index and average inter-patch length) based on the Landscape Function Analysis method of surveying rangelands. The response patterns of all five indicators were highly variable across the sampled piospheres, and did not correspond well with the conceptual piosphere model. There was also no systematic effect of waterhole closure on vegetation patchiness. For three indices of landscape function – nutrient cycling, infiltration and soil stability – the responses to distance from water were similarly variable, and there was no significant effect of waterhole closure. The lack of clear piosphere patterns in this study, in contrast to earlier piosphere studies in the Kruger National Park, was attributed to high rainfall and the different patterns of animal utilization during wet periods when forage and naturally-occurring drinking water is abundant.

Key words: piospheres, thresholds, resilience, recovery, Landscape Function Analysis

5.1 INTRODUCTION

Patchiness and ecosystem function

The development of patches (areas with distinctive vegetation structure and composition) in grazed rangeland is a common phenomenon (Kotliar & Wiens 1990; Tongway & Ludwig 1990; Ludwig *et al.* 2000; McIvor *et al.* 2005). Patchiness has been linked to ecosystem function, or the ability of the ecosystem to carry out vital processes such as nutrient cycling and soil and water conservation (McNaughton *et al.* 1989; Ludwig & Tongway 2003; Tongway & Hindley 2004a; b). The role of patchiness in contributing to ecosystem heterogeneity and the maintenance of biodiversity and resilience (the amount of disturbance the ecosystem can absorb before changing state - (Gunderson 2000)) at a range of scales is of increasing interest in protected area management (Stalmans *et al.* 2001; Rogers 2003; Van de Koppel & Rietkerk 2004; Van Nes & Scheffer 2005).

The functionality of landscapes depends on the distribution of “run-on” patches in the landscape that can capture and retain resources, relative to “run-off” inter-patch or matrix areas that lose resources (Ludwig *et al.* 2000). In savannas characterized by a mosaic of vegetated patches and bare inter-patches, the primary pattern-inducing process is that of redistribution – excess water (from rainfall) moves over the landscape as run-off, which vegetated patches capture as run-on. These patches also trap the soil, nutrients, organic matter and seeds contained in run-on water (Ludwig *et al.* 2000). This redistribution of resources from the matrix to vegetated patches results in better soil water infiltration, enhanced soil nutrient status and higher recruitment of plants in the patches themselves. Vegetated run-on patches should thus have enhanced ecosystem function relative to adjacent bare areas and they should grow and maintain themselves as they assimilate these resources into biomass, for as long as the patch remains physically intact.

Ludwig *et al.* (2000) noted that all landscapes exist on a continuum from dysfunctional (“leaky”) to highly functional (“conserving”), and that disturbances such as fire, trampling and grazing can make systems more leaky, by removing vegetation that can trap resources. The distribution and size of patches in a landscape have clear implications for resilience: many, large patches and small inter-patches will place a system on the “conserving”, functional end of the continuum. Systems with few/small patches and large inter-patches will fall on the “leaky”, dysfunctional side of the spectrum. Thus, understanding the response of an ecosystem to a

perturbation (such as intense herbivore utilization) and its implications for biodiversity and resilience conservation should include some consideration of patchiness and function.

Artificial water provision and piospheres in the Kruger Park

Artificial water provision is a key management tool in protected savanna areas, particularly in fenced systems such as the Kruger National Park (KNP) (Owen-Smith 1996; Gaylard *et al.* 2003). Where natural perennial water is sparsely distributed, artificial point water-sources act as agents of large mammalian herbivore concentration, resulting in the formation of piospheres (van der Schijff 1959; Lange 1969; Thrash 1993; Adler & Hall 2005). In the simplest case of a single water point in a uniform rangeland type, a gradient of herbivore utilization develops that is greatest near the waterhole and declines with distance from the waterhole, creating characteristic zones of herbivore impact (Thrash & Derry 1999).

The implications of altered herbivore utilization, within the context of piospheres, for patch creation and altered ecosystem function, are clear: drinking water attracts herbivores into an area, and they focus their foraging close to that water source. Selective choices of forage by the herbivores result in a mosaic of vegetation of varying heights. Patches of closely-cropped grass initially result from forage preferences (e.g. for the most palatable species) being perpetuated, and a positive feed-back loop is created. Herbivores may be continually attracted back to these initial patches by the high quality, productive herbage that re-grows after defoliation and dung deposition, and a grazing lawn may emerge (McNaughton 1984; Milchunas *et al.* 1988; Karki & Jhala 2000; McIvor *et al.* 2005). Within the sacrifice zone of a piosphere (Andrew 1988; Thrash & Derry 1999), these short patches are those in which the symptoms of over-utilization by herbivores (plant mortality, erosion and reduced infiltration capacity) first become evident. A mosaic of small, highly fragmented short patches dominated by annual plants emerges within a matrix of bare inter-patch areas.

Gradients of patch type and size superimpose themselves over the distance-from-water gradient of a piosphere. Van der Schijff (1959) surveyed vegetation around water points in the Kruger National Park and identified five utilization zones. A trampled sacrifice zone denuded of vegetation occurred close to the waterhole (0 – 91 m), followed by a zone characterized by a mosaic of short patches and bare areas (up to 1.6 km). The third zone (extending p to 5 km from the water point) had uniformly grazed short grass (a lawn), a fourth zone (up to 8 km) was

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characterized by lightly, selectively-grazed patches interspersed with tall unutilized vegetation and the fifth zone (beyond 8 km from water) by tall unutilized vegetation. At the time of this study, large parts of the KNP were further than 16 km from water, and therefore little utilized by water dependent herbivores. A second piosphere study in the KNP in 1990 (Thrash 1993) found only the first three of these zones. By 1990, most of the rangeland in the KNP was within 10 km of permanent water (Thrash 1993). Thrash (1993) described the disappearance of the two outermost piosphere zones as evidence that habitat diversity may have been adversely affected by artificial water provision in the KNP.

If artificial water provision, as an indirect source of herbivore-mediated disturbance, represents an agent of ecosystem change that acts on both biotic and abiotic components of a savanna ecosystem, then the research challenge is to quantify the relationship between water provision and different attributes of heterogeneity, in a spatially- and temporally-explicit manner. Achieving this would allow managers to integrate artificial waterhole management (e.g. waterhole closure, either temporary or permanent) when setting goals for heterogeneity management.

The goal of this study was to document the responses of patch size and distribution and ecosystem function (nutrient cycling, soil stability and infiltration) along herbivore utilization gradients within piospheres in the Kruger National Park (KNP). Since the late-1990s, managers in the KNP have been closing waterholes, in an attempt to restore historical herbivore utilization patterns (Gaylard *et al.* 2003). Elucidation of the relationship between artificial water provision and the maintenance of resilience in the KNP requires detailed knowledge of the functional gradients associated with active or recovering (i.e. waterhole closed) piospheres. The specific questions we addressed in this study were:

1. How does ecosystem function and patchiness change along distance-from-water gradients?
2. Does waterhole status (open or closed) affect the response of ecosystem function and patchiness to distance from water?
3. How do different patch types (patches dominated by different growth forms) differ with respect to function?

Based on the piosphere model, we predicted the following:

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1. Total patch area would increase with distance from water, peaking where grazing lawns occur, because the vegetation resembles a single large patch (McNaughton 1984).
2. Waterhole closure should result in larger patches (relative to active piospheres), following re-establishment of perennial vegetation in the sacrifice zones.
3. Patch frequency, which together with patch size contributes to total patch area, should be low near the waterhole (where heavy herbivore utilization and trampling occur) and where grazing lawns are present.
4. Landscape function (leaky versus conserving) would correlate positively with vegetation patchiness. Bare soil patches (hereafter referred to as inter-patches) should have lower function than vegetated patches, and larger vegetated patches should have greater function than smaller patches. We thus predicted that function would be lowest close to the waterhole, and peak at intermediate distances from water.
5. Function should increase around closed waterholes relative to open waterholes.

5.2 METHODS

Data collection

Eleven waterholes from the Skukuza, Satara, Letaba and Phalaborwa land systems (Venter 1990) of the Kruger National Park (Fig. 2.1) were surveyed using the Landscape Function Analysis (LFA) techniques of Tongway and Hindley (2004a). These piospheres were selected because they had been previously surveyed, for a range of soil and vegetation parameters (Thrash 1993), before waterhole closure commenced in the KNP. The location and current status of each waterhole is summarised in Table 5.1.

The Satara and Letaba land systems are characterized by clayey soils derived from basalt. The Satara land system consists of fine-leaved tree savanna dominated by *Acacia nigrescens*, *Dichrostachys cinerea* and *Sclerocarya birrea* (Venter *et al.* 2003). The Letaba system is associated with *Colophospermum mopane* shrubveld, although *Combretum imberbe* is also abundant (Venter *et al.* 2003). The Satara land system receives higher rainfall than the Letaba system, and is thus characterised by higher perennial grass cover.

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The Skukuza and Phalaborwa land systems are underlain by granitic rocks and have distinctive catenal soil gradients. In the Skukuza land system, the vegetation of the sandy uplands included dense sands of deciduous *Combretum* spp. and *Terminalia* spp. The foot-slopes, where duplex soils are common, are characterised by more open, small-leaved, thorny shrub, in which several species of *Acacia* and *Albizia* occur along with *Dichrostachys cinerea*, *Euclea* spp., and *Combretum hereroense*. Grasses abundant on the foot-slopes tend to be nutritious bulk-growers. Seepines are dominated by *Terminalia sericea* and *Combretum zeyheri*, and water-loving sedges and grasses such as *Eragrostis gummiflua*. Grass cover in the land system as a whole tends to be sparse, especially in dry years, but may be moderate to dense in wet periods (Venter *et al.* 2003).

The Phalaborwa land system is characterised by *Combretum apiculatum* and *Colophospermum mopane* bushveld (Venter *et al.* 2003). *C. apiculatum* typically occurs on the shallow gravels and sandy soils on the crests, whereas *C. mopane* grows in the clayey soils of the foot-slopes (duplex soils) and along dolerite dykes.

Table 5.1. The dates (month and year) of opening and closure of the eleven artificial waterholes surveyed in 2006, with current status given

Land type	Site	Current status	Date opened	Date closed
Skukuza	Manzimhlope	Open	01/1933	
	Timbiteni	Open	01/1962	
	Shiteve-teve	Open	05/1973	
Satara	Witpens	Open	unknown	
	Mananga	Open	07/1973	
	Marheya	Closed	07/1962	Structure removed 2001
Phalaborwa	Shivulani	Open	01/1935	
	Marhumbeni	Closed	07/1970	Structure removed 2001
	Wik-en-Weeg	Closed	1973	Unknown (assumed 2001)
Letaba	Capricorn	Closed	02/1975	Original structure removed 2001, roan enclosure completed 2002. Waterhole reopened 2002.
	Tihongonyeni	Open	04/1962	

At each waterhole, LFA transects were laid at the edge of the waterhole (0 m), and at 25, 50, 75, 100, 200, 300, 400, 500, 1000, 2000, and 5000 m from the waterhole. At each sampling distance, we laid out a 50 m tape measure and recorded the distances at which perennially

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vegetated patches intercepted it. Thus, we measured the length of each patch and inter-patch (bare, un-vegetated patch). In addition, we recorded the average width (up to a maximum of 10 m on either side of the tape measure) of each patch and inter-patch. These data were used to generate indices of patchiness, using a Microsoft Excel-based spreadsheet designed by Tongway and Hindley (2004b). Patch frequency was calculated as the average number of patches per 10 m transect and patch area index was derived by dividing the total patch area by the maximum area. Landscape organization index was derived from the division of the sum of the patch lengths by the length of the transect line.

We identified patch types in the field, by classifying each vegetated patch according to the dominant growth form present in each patch (bare soil, grass, shrubs, trees, forbs). Inter-patches (bare soil patches) were identified as areas of bare soil where no perennial plants were rooted and where resources such as water, soil materials and litter can be freely transported over the soil surface (Tongway & Hindley 2004b). In LFA, annual vegetation is classified as litter (Tongway & Hindley 2004b). Grass patches were classified as those vegetated patches containing perennial grasses, where no shrub or tree was present. Patches containing only a single shrub/tree, were classified as shrub or tree patches, respectively. For complex patches (i.e. consisting of more than a single tussock of grass) consisting of perennial grasses and one or more shrubs, the patch was classified as a shrub patch. Patches consisting of trees and grasses were similarly classified as tree patches. For each patch type present on a transect, three representative patches were selected and assessed using the eleven landscape function criteria formulated and described by Tongway and Hindley (2004b). Each criterion assesses the status of a specific soil surface process. The eleven scores were variously combined to derive three landscape function indices (infiltration capacity, nutrient cycling and stability or resistance to soil erosion), the values of which represent a percentage of a maximum potential score (Tongway & Hindley 2004b).

Data Analysis

We fitted generalized additive models (GAMs) to examine the change in each index of patchiness and landscape function with distance-from-water (ter Braak & Smilauer 1997). GAMs combine (Hastie & Tibshirani 1990) elements of generalized linear models (GLMs) and additive models (Quinn & Keough 2002), and each predictor is a non-parametric smoothing function.

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Scatter-plot smoothers, such as Lowess or cubic splines, are used to obtain a smooth generalization of the relationship between predictor and response variables (Hastie & Tibshirani 1990; Quinn & Keough 2002). Various distributions for the dependent variable can be accommodated, and a range of functions can be used to link the expected values of the dependent variable and the values of the predictor variable. We specified a normal distribution with an identity link function, and considered models with three or fewer smoothing functions. Akaike's Information Criteria (AIC) were used to select the most likely model for each dataset.

We compared open and closed sites by calculating the area under the curve (AUC) for each site. Because GAMs could not be fitted to all sites for each patchiness variable, AUC was calculated from a scatter plot of the data (i.e. not using the fitted models). The AUC represented a single, integrated value for each site (thus overcoming problems with independence), and open and closed waterholes were compared using a t-test (equal variances not assumed) for each landscape function index.

The total area covered by all the patches identified on a transect were added to obtain the total patch area for the transect, and percentage of that area covered by each patch type was calculated to obtain the overall contribution of each patch type on the transect. The contribution (%) of each different patch type to total patch area were plotted along the distance-from-water piosphere gradients for each site. In addition, we examined the average function scores ($\% \pm \text{SE}$) for each patch type, along the distance-from-water gradient, for each site. We contrasted the functionality of bare inter-patches relative to perennially vegetated patches (grass-, shrub-, tree- and forb- dominated patches), using a Kruskal-Wallis test for each variable.

5.3 RESULTS

Vegetation patchiness

Patch frequency and patch area index did not respond consistently to distance from water and no clear piosphere patterns emerged. Landscape organization index also had a variable response to distance from water, but tended to increase as distance from water increased (see Fig. 5.1). Some sites (5 sites) had small (0- 25 m) apparent sacrifice zones, but no other piosphere zonation was present. Average inter-patch length also varied in its response to distance-from-water across the study sites, although the general pattern was one of smaller inter-patches further

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from water (1000 – 5000 m) than near water (0 – 500 m) (Figure 5.2). There was no effect of closure for any of these four patchiness indices (range in $t = 0.16$ to 0.86 , range in $df = 6.29$ to 8.83 , range in p values = 0.42 to 0.87).

The contribution of different patch types (those dominated by different dominant growth forms) to total transect area was the patchiness variable most consistent with the conceptual piosphere model, especially with respect to bare ground. Bare soil was most abundant close to the waterhole at most sites and less abundant further from water (Figure 5.3 a, b). At some sites (5 sites), there was an abrupt transition from a zone dominated by bare ground (sacrifice zone) to a zone dominated by vegetated patches (Figure 5.3a), while at other sites (6 sites) the decline was slower and no distinct bare zone was apparent (Figure 5.3b). The data shown in Figure 5.3 come from the Shiteve-teve and Timbiteni waterholes; these were chosen as representative of the two common piosphere patterns described above. At all sites, there appeared to be two distinct piosphere zones. The first zone was either dominated by a uniform contribution of different patch types along the distance gradient (Figure 5.3a) or by a gradual increase in vegetated patch areas with distance from water (Figure 5.3b). The second was characterised by high patch heterogeneity. Trees contributed significantly to area (10 – 40 %) only beyond 1000 m from water. A similar pattern was attributed to tall grass cover – this tended to increase in abundance as distance from water increased, only contributing more than 10 % cover beyond 1000 m. Short grass had the approximately opposite pattern, only contributing significantly to cover up to approximately 10 – 100 m from water. There were no distinct patterns associated with either open or closed waterholes.

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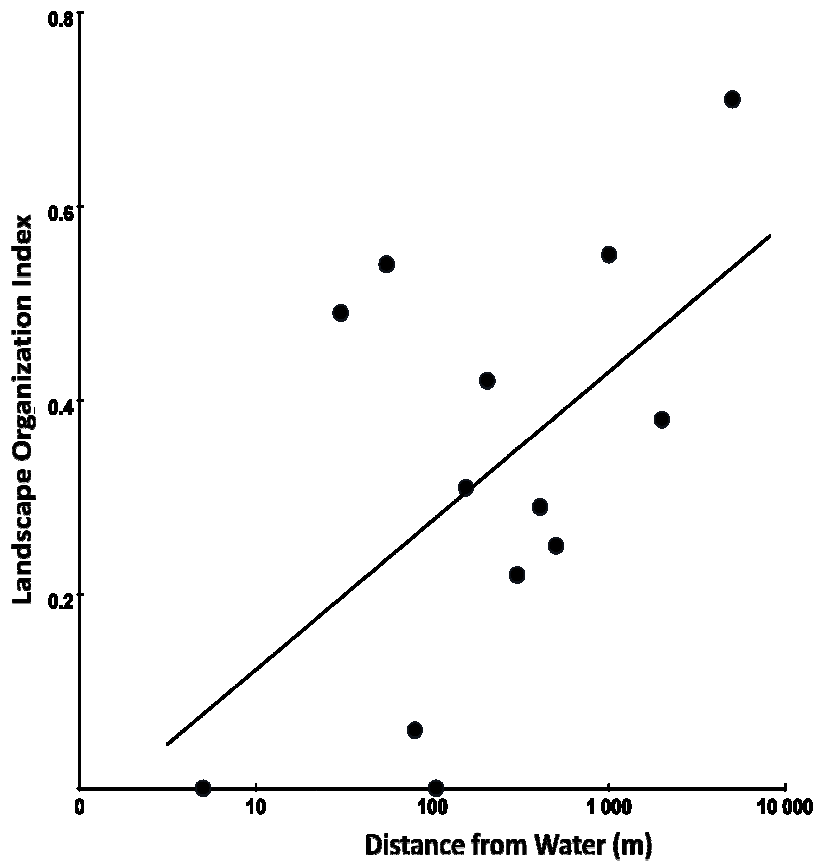


Fig. 5.1. The typical response of landscape organization index (sum of patch lengths divided by total transect length) to distance from water, from the Mananga waterhole. Dots represent actual observations, the solid line the fitted GAM.

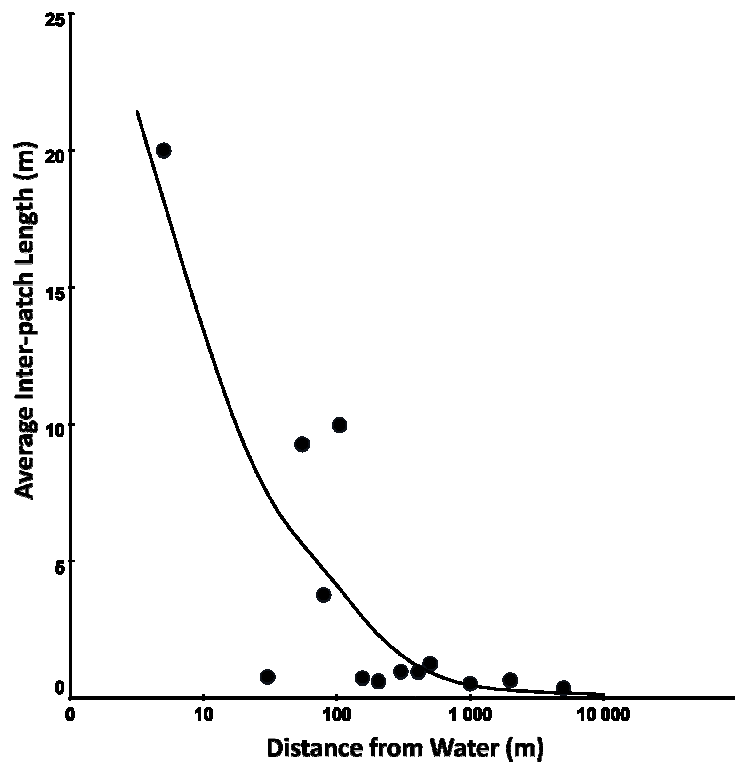


Fig. 5.2. The typical response of landscape organization index (sum of patch lengths divided by total transect length) to distance from water, from the Mananga waterhole. Dots represent actual observations, the solid line the fitted GAM.

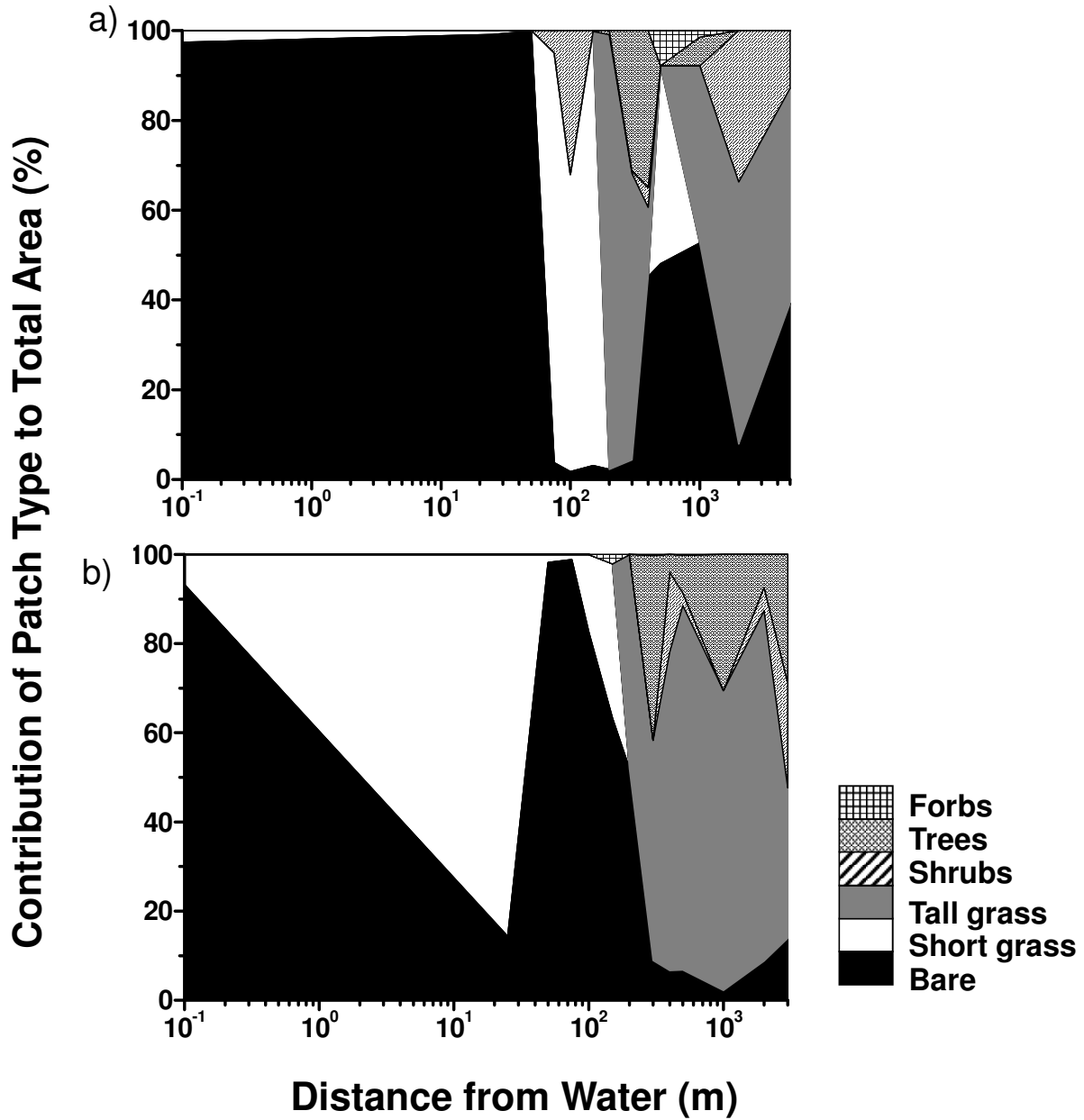


Fig. 5.3. The change in the distribution of inter-patches and different patch types along distance-from-water gradients in the KNP, showing two typical responses: a) discrete sacrifice zone with sharp boundary (from the Shiteve-teve waterhole) and b) gradual decline in contribution of bare inter-patches in first piosphere zone (from the Timbiteni waterhole).

Landscape function

Neither infiltration nor stability (resistance to soil erosion) responded consistently to distance from water – no clear piosphere gradients were found, contrary to our predictions. There were two general response patterns of nutrient cycling to distance from water (Fig. 5.4): 1) highest function scores recorded at intermediate distances from water (5 sites) and 2) an increase in function with distance from water (6 sites). The data presented in Figure 5.4 come from the Witpens and Timbiteni waterholes. These sites are presented because they clearly display the common patterns found at other sites. There was no significant effect of waterhole closure for any of the three landscape function indices (range in t values = 0.33 to 1.66, df = 5.06 to 8.45, range in p values = 0.16 to 0.75). For all three landscape function indices, patch type had a significant effect on landscape function (range in χ^2 = 78.932 to 248.793, df = 4, $p \leq 0.001$). Bare patches had the lowest function scores for all three indices, and the general trend was for highest functionality in tree-dominated patches, followed by shrub-dominated patches and then grass-dominated patches.

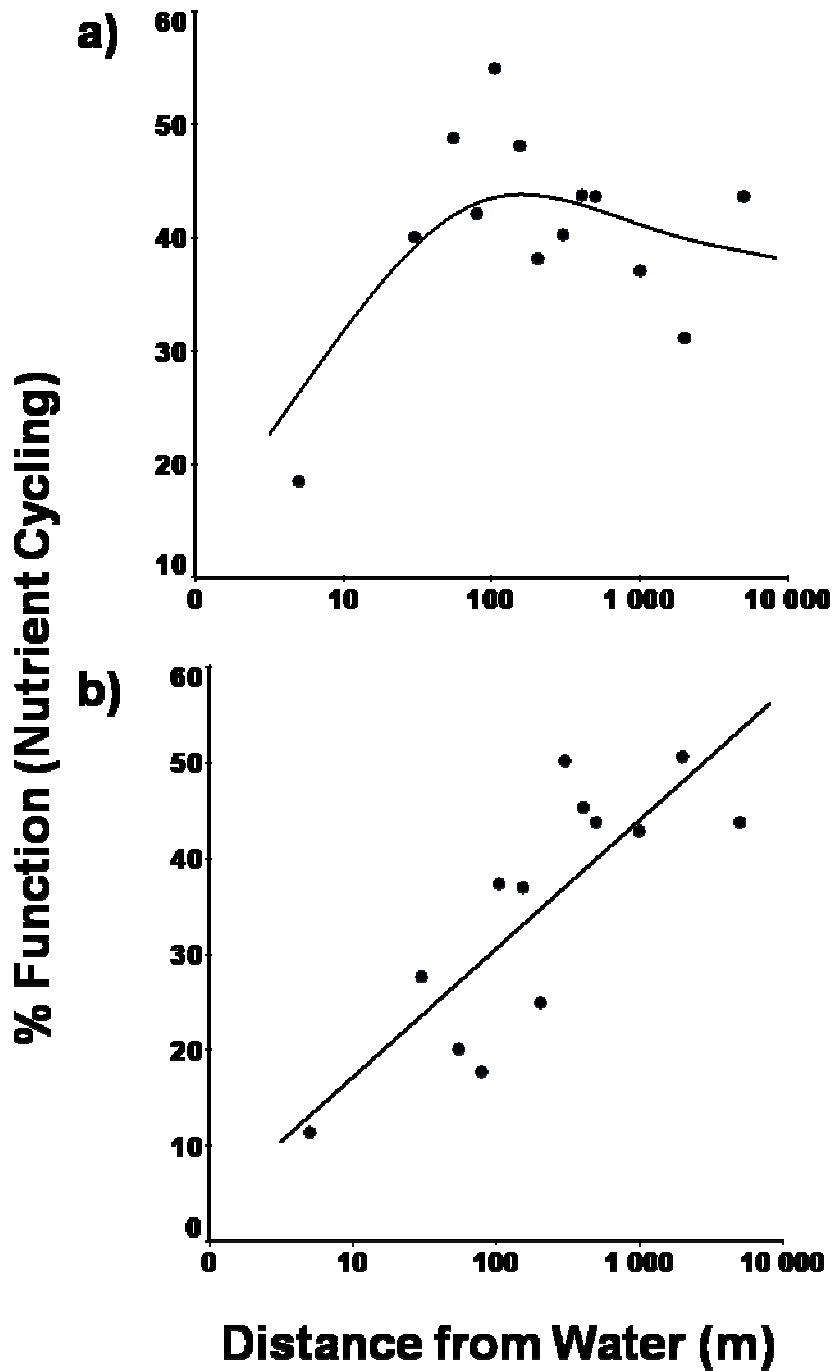


Fig. 5.4. The two typical responses of nutrient cycling function to distance from water: a) positive quadratic response (Witpens waterhole) and b) general, approximately linear increase (Timbiteni waterhole).

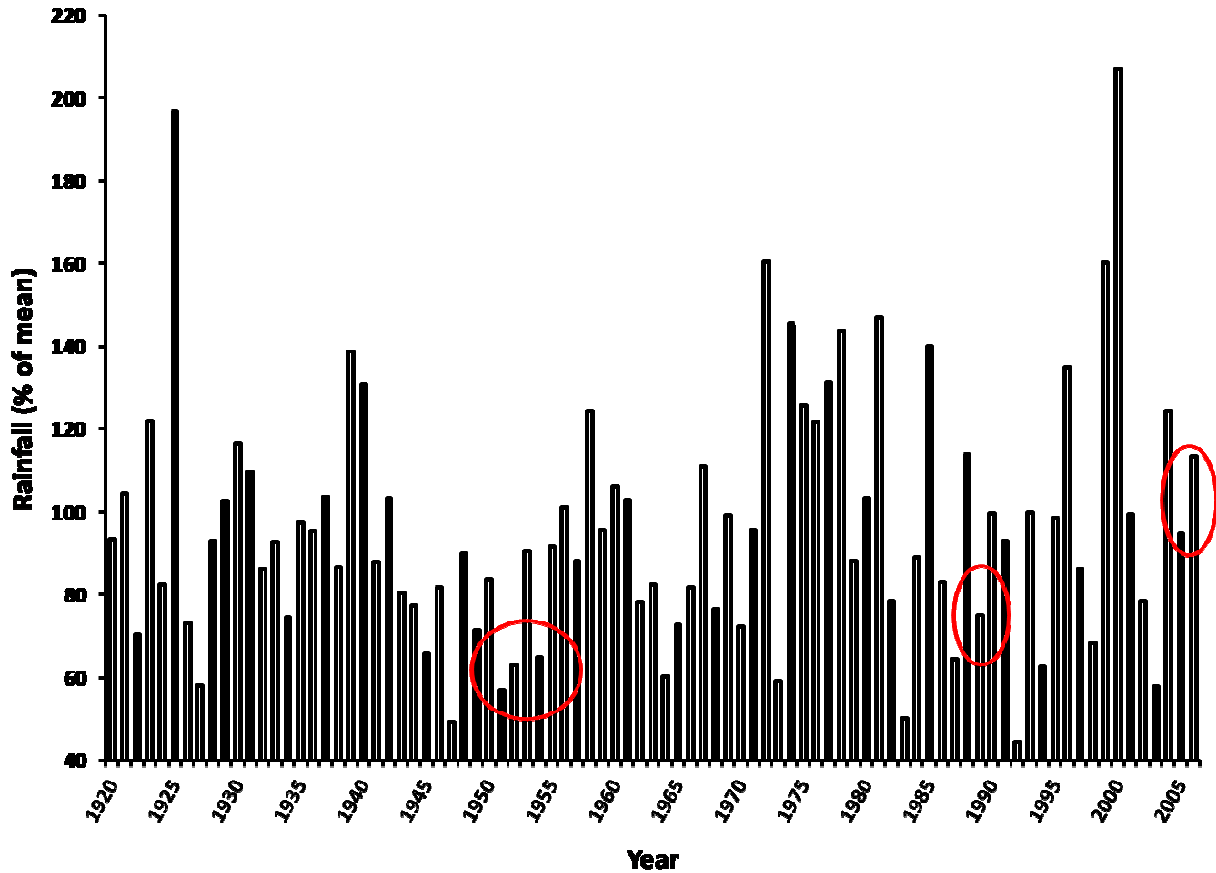


Fig. 5.5. The change in annual wet season (July – June) rainfall (solid line), as a % of the long-term average, between 1950 and 2006. The three study periods (1950-1955, 1989-1990 and 2005-2006) are indicated by circles.

5.4 DISCUSSION

Artificial water provision has been a source of concern to both ecologists and managers in the KNP since the water-for-game programme commenced in the 1930s (Pienaar 1983; Joubert 1986; Gaylard *et al.* 2003). There has, however, been a paradigm shift away from managing to promote uniform savanna utilization by herbivores, based on the carrying capacity concept, to the current focus on managing to promote heterogeneity at all spatio-temporal scales (Rogers 2003). With this shift has come a change in the way artificial water provision is regarded. Initial concerns centered on preventing herbivore population crashes during droughts and encouraging more uniform savanna utilization by herbivores. This caused causing widespread vegetation

homogenization and a potential loss of biodiversity (Thrash 1993; Gaylard *et al.* 2003). The current study comes in response to a policy reversal in the late-1990s (Pienaar *et al.* 1997): artificial waterholes in the KNP are now being closed, as part of an attempt to promote heterogeneity and the conservation of biodiversity and ecosystem resilience. Here, we specifically address the functional response of the ecosystem to artificial water provision and waterhole closure.

Both van der Schijff (1959) and Thrash (1993) previously recorded very clear, zonal piospheres in the KNP. The use of LFA in this study, both with respect to patterns of patchiness and landscape function, has indicated that the piosphere response in 2007 was weak. For soil water infiltration rate, distinct sacrifice zones extending 40 – 100 m from the waterholes were recorded in 1990 (Thrash 1993), whereas the same sites in the current study had no distinct sacrifice zones, and no clear piosphere gradients. The intensity of the piosphere effect was lower in 2007, compared to 1990, regardless of waterhole status (active or recovering).

Both previous studies on piospheres in the KNP (van der Schijff 1959; Thrash 1993) were undertaken during drier periods than the current study (Fig. 5.5), which suggests that there has been a positive response to recent (post-2000) rainfall inputs. The implication, therefore, is that artificial water provision at the chosen study sites has not forced the rangeland over a permanent functional threshold, leaving ecosystem resilience intact.

Fine-scale patchiness occurs during periods of sufficient rainfall, and the run-on/run-off process operates at the scale of individual grass tufts and inter-tufts. During dry periods, these processes operate at a broader landscape scale. The scale at which structural and functional heterogeneity is expressed in the KNP should therefore track climatic variability under relatively light herbivore densities such as in the KNP (East 1984; Mills & Funston 2003; Peel 2009), as patches expand and contract, provided ecosystem resilience remains intact. Our study showed no effect of waterhole closure on patchiness and ecosystem function, but given the lack of clear piosphere patterns in the current study, it is difficult to conclude that this indicates compromised resilience. On the contrary, piosphere intermittency and the lack of a closure effect suggest that climate is having a relatively stronger effect on vegetation structure and soil function than grazing (Ellis & Swift 1988; Behnke & Scoones 1993; Vetter 2004). The relatively low herbivore biomass in the KNP also contributes to the temporary nature of the piosphere effect. The challenge is to test this hypothesis in more heavily stocked savannas, and determine under

what conditions ecosystem resilience and heterogeneity is compromised by artificial water provision.

This study highlights the value of LFA as a piosphere monitoring technique. As a rapid assessment technique, LFA has the potential to replace time-consuming and expensive laboratory-intensive conventional methods of assessing the state of the soil surface (vegetative cover, soil nutrient status, resistance to erosion and ability to retain water and other resources), and the data collected in this study can serve as a baseline for future monitoring of the effect of artificial water provision and waterhole closure on vegetative cover and soil surface integrity.

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CHAPTER 6: ASSESSING HERBIVORE IMPACTS AND PIOSPHERE RECOVERY BY REMOTE SENSING IN THE KRUGER NATIONAL PARK

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Abstract Water provision is an important management intervention in savanna ecosystems, and has important implications for soil and vegetation resilience. We investigated the feasibility of using a remote-sensing approach to detect the recovery of vegetation around closed waterholes in the Kruger National Park. We selected 58 waterholes, incorporating both active and closed boreholes, distributed over the park, and calculated the normalized difference vegetation index (NDVI) at different distances from water for two time periods (2000 and 2006), from Landsat 7 satellite (Enhanced Thematic Mapper plus sensor). We also compared NDVI at open and closed waterholes, at different distance from water. NDVI responded significantly to distance from water, with the most common biosphere response being an increasing NDVI along the grazing gradient. Rainfall in 2000, when waterhole closure was initiated, was higher than in 2006 (post-closure), which resulted in significantly higher NDVI in 2000 compared to 2006. There was no significant vegetation recovery around closed waterholes, and the relative decline in NDVI between 2000 and 2006 was not influenced by underlying geology (basalt vs. granite) or long-term mean annual precipitation. Our findings show that satellite images provide a useful tool to monitor biosphere dynamics at a broad landscape scale.

Key words: NDVI, vegetation indices, grazing gradient, vegetation recovery, resilience

6.1 INTRODUCTION

The provision of artificial point water sources in rangelands result in the development of “piospheres” (Graetz & Ludwig 1978; Andrew 1988; Thrash & Derry 1999). Radial herbivore movement between drinking and foraging locations results in an increasing gradient of herbivore impact (trampling, grazing, browsing) around water points, defined as a piosphere (Lange 1969). Piosphere patterns have been documented for a range of soil and vegetation parameters, including vegetation cover, biomass and species composition, soil compaction, infiltration rates and soil nutrient cycling and herbivore track density (Thrash 1993; James *et al.* 1999; Heshmatti *et al.* 2002; Landsberg *et al.* 2003). Past studies have investigated the response of vegetation indices such as NDVI to the grazing gradient in piospheres around artificial waterholes, and these remote-sensed indices usually increase as distance from water increases, although the intensity of the piosphere response is strongly influenced by rainfall (Pickup *et al.* 1994a; Harris & Asner 2003; Lind *et al.* 2003; Washington-Allen *et al.* 2004).

Remote-sensing techniques are useful for qualitatively and quantitatively assessing vegetation patterns in rangeland ecosystems. The speed and accuracy of ecological monitoring can be increased by using image-based (remote-sensing) methods (Booth & Cox 2008). For areas larger than 200 ha, image-based methods are more cost-effective than intensive ground-based methods and allow uniform, high density sampling in place of judgement-based choices of representative area for ground-based studies (Booth & Cox 2008). Savanna landscapes are typically highly spatially variable, animal utilization is non-uniform and water and soil redistribution processes resulting in patchy vegetation distribution common, and the potential for error from a limited number of point assessments is therefore large (Pickup *et al.* 1994b). The logistic problems of working at a landscape-scale are solved by remote-sensing approaches (Pickup *et al.* 1994b; Saltz *et al.* 1999).

Visible and near-infra-red images are the most useful data to examine vegetation patterns and the corresponding ecological processes at large scales (Saltz *et al.* 1999). Vegetation indices such as the Normalized Difference Vegetation Index (NDVI), derived from such remotely sensed data, have frequently been used to predict green biomass and vegetation cover (Wallens 1997; Paruelo *et al.* 1999; Wylie *et al.* 2002), by comparing the absorption of light in the red part of the visible spectrum by chlorophyll pigments with the high reflectivity of plant materials in the near-

infra-red spectrum (Tucker 1979; Gamon *et al.* 1995). In this study, we use NDVI images derived from Landsat 7 ETM+ (Enhanced Thematic Mapper plus sensor) satellite images to examine the response of vegetation to artificial water provision and waterhole closure in the Kruger National Park (KNP). The KNP has a long history of artificial water provision for game. The first artificial waterholes were established in the park in the early 1930s (Joubert 1986; Gaylard *et al.* 2003). This programme aimed to stabilize herbivore populations during drought periods (Pienaar 1983; Gaylard *et al.* 2003). By the early 1990s, less than 20 % of the land area of the KNP was further than 5 km from a perennial water source (Gaylard *et al.* 2003), yet the anticipated benefits of artificial water provision did not materialize (Thrash 1993; Gaylard *et al.* 2003). Herbivore population crashes during droughts were intensified following artificial water provision, and rare antelope populations crashed to unprecedented levels during the drought of 1982 – 1987 (Harrington *et al.* 1999; Grant *et al.* 2002). Artificial water provision was implicated in the reduction of herbivore diversity over large areas of the KNP, following the range expansions of common water-dependent herbivore species (e.g. wildebeest and zebra), and their main predators (lions) that occurred at the expense of the rarer herbivore species after water provision (Owen-Smith 1996). In addition, widespread vegetation and soil homogenization was linked to artificial water provision (Thrash 1993; Gaylard *et al.* 2003). As a result, the policy of widespread artificial water provision was halted in the mid-1990s (Pienaar *et al.* 1997), and a large proportion of the artificial waterholes in the KNP have now been closed. This policy reversal follows a change of management paradigm in the KNP, from past objectives of suppressing variability to the current goal of maintaining and promoting heterogeneity at all spatio-temporal scales (Gaylard *et al.* 2003).

We ask the following questions in this paper:

1. Is NDVI a useful indicator of biosphere dynamics?
2. Has waterhole closure resulted in vegetation recovery (i.e. an increase in NDVI)?
3. Is vegetation recovery around closed waterholes mediated by geology and rainfall?

This remote-sensing approach to studying biosphere dynamics in the KNP concludes an intensive study of the responses of soil and vegetation variables to artificial water provision and waterhole closure in the KNP (Chapters 3 – 5, this thesis). Previous ground-based biosphere surveys conducted in the 2006 growing season at eleven waterholes, six years after waterhole

closure, suggested that although soil and vegetation resilience was not negatively impacted by long-term artificial water provision in the KNP, the recovery of vegetation and soil around artificial waterholes was limited (Chapters 3 – 5, this thesis). Here, we use remote sensing to overcome the limitations of ground-based surveys and test the generality of this conclusion, as part of an effort to assess the outcome of the waterhole closure policy in the KNP.

6.2 METHODS

Remote sensing

Fifty-eight artificial waterholes, comprising 22 open sites and 36 closed sites, were selected in the KNP. The selected waterholes represent both major geologies of the KNP (basalts and granites). Waterholes had to be at least 4 km distant from the closest neighbouring waterhole, river or dam to be selected. Three buffer zones (0 – 150 m, 150 – 500 m and 500 – 2000 m) were created around each waterhole. In the buffer zone close to each waterhole, 15 random sampling points spaced at least 30 m apart were created; 30 points were placed in each of the remaining buffer zones. We used four Landsat 7 ETM+ satellite images (Table 6.1) with a spatial resolution of 30 m to calculate NDVI (Rouse *et al.* 1974) for each sampling point, using the following equation:

$$\text{NDVI} = (\text{NIR} - \text{R}) / (\text{NIR} + \text{R}),$$

where NIR is the near infra-red wavelengths ($\pm 0.8 - 0.9 \mu$ or band 4) and R the visible red ($\pm 0.6 - 0.7 \mu$ or band 3) wavelengths. NDVI can theoretically take values between -1 and 1, with positive values indicating green, vegetated surfaces, and increases in NDVI indicating an increase in vegetation greenness (Weis *et al.* 2004). Negative NDVI values indicate non-vegetated surfaces such as bare soil. NDVI was calculated for 4 April 2000 and 12 May 2006. The satellite images represent the end of the growing season (April-May) in the KNP. This period avoids potential problems caused by differences due to immediate grazing pressure (Pickup & Chewings 1994). We performed an atmospheric correction of the Landsat images used in this analysis, but there was no difference between the NDVI values obtained before and after correction, and we thus proceeded with the unmodified images. Mean annual rainfall across

the entire KNP in the season (1 July to date of image) preceding the image was higher in 2000 (1114 mm) than 2006 (638 mm). We selected the images from 2000 because they correspond to the approximate date of waterhole closure in the KNP, and the 2006 images correspond to ground-based surveys around a subset of the selected waterholes.

To overcome the lack of independence of points from the same site, we derived a relative NDVI piosphere index by subtracting the mean NDVI for the 0 – 150 m buffer (i.e. near each waterhole) from the mean NDVI for the 500 – 2000 m buffer (i.e. far from each waterhole), and then subtracting this measure of piosphere effect for 2000 from the same measurement in 2006 for each site. Thus, a single index was derived for each site, representing a measure of the temporal change in slope of NDVI along the piosphere gradient at each site.

Table 6.1. The scene identity codes of the images used

Image Date	Region	Scene ID
4 April 2000	Northern KNP	L71168076_07620000409
	Southern KNP	L71168077_07720000409
12 May 2006	Northern KNP	L71168076_07620060512
	Southern KNP	L71168077_07720060512

Data analysis

We compared the NDVI in 2000 and 2006 for each sampling point using a paired sample t-test. Likewise, we tested the effect of distance on NDVI for both years by comparing mean NDVI close to water (0 – 150 m) with mean NDVI far from water (500 – 2000 m) for each site, using a paired sample t-test . We developed a generalized linear model (GLM) of the response of the relative NDVI piosphere index to waterhole status (open and closed), geology (granite and basalt), long-term mean annual precipitation (MAP) and all two- and three-way interactions. The effect of geology on NDVI for both years was tested using one-way ANOVA, and we tested the relationship between NDVI and long-term MAP using Pearson’s correlation analysis.

6.3 RESULTS

NDVI in 2006 was significantly lower than NDVI in 2000 (Fig. 6.1), over all 58 waterholes ($t = 211.55$, $df = 4340$, $p < 0.001$). This corresponded to lower rainfall in 2006 (average rainfall across the whole KNP from 1 July 2005 – 30 April 2006 = 638 mm) compared to 2000 (average rainfall 1 July 1999 – 30 March 2000 = 1114 mm). Mean NDVI close to water (0-150 m) was also significantly lower than mean NDVI far from water (500 – 2000 m) in both 2000 ($t = 1.86$, $df = 57$, $p = 0.068$) and 2006 ($t = 1.794$, $df = 57$, $p = 0.078$), although many sites also had an inverse biosphere pattern or had maximum or minimum NDVI at intermediate distances from water (Table 6.2).

Waterhole status (open and closed), geology (granite and geology) and long-term MAP did not significantly ($p > 0.05$) affect the relative NDVI biosphere index, individually or in combination, nor were there any significant interactions ($p > 0.05$). NDVI itself was significantly higher on basaltic soils (mean₂₀₀₀ = 0.403, mean₂₀₀₆ = 0.047) than on granitic soils (mean₂₀₀₀ = 0.377, mean₂₀₀₆ = 0.025) for 2000 ($F = 7.72$, $df = 173$, $p = 0.006$) and 2006 ($F = 4.42$, $df = 173$, $p = 0.037$) (Fig. 6.2), and was significantly but weakly positively correlated with long-term MAP (r_p 2000 = 0.031, $p = 0.039$; r_p 2006 = 0.119, $p < 0.001$).

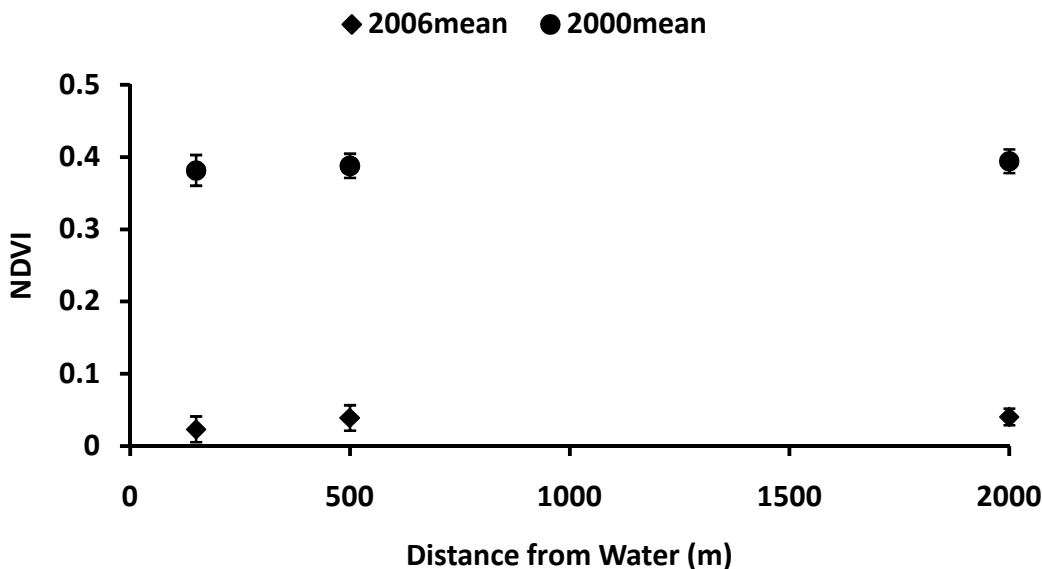


Fig. 6.1. The difference in NDVI between 2000 and 2006, at different distances from water. Vertical bars represent 95 % confidence intervals.

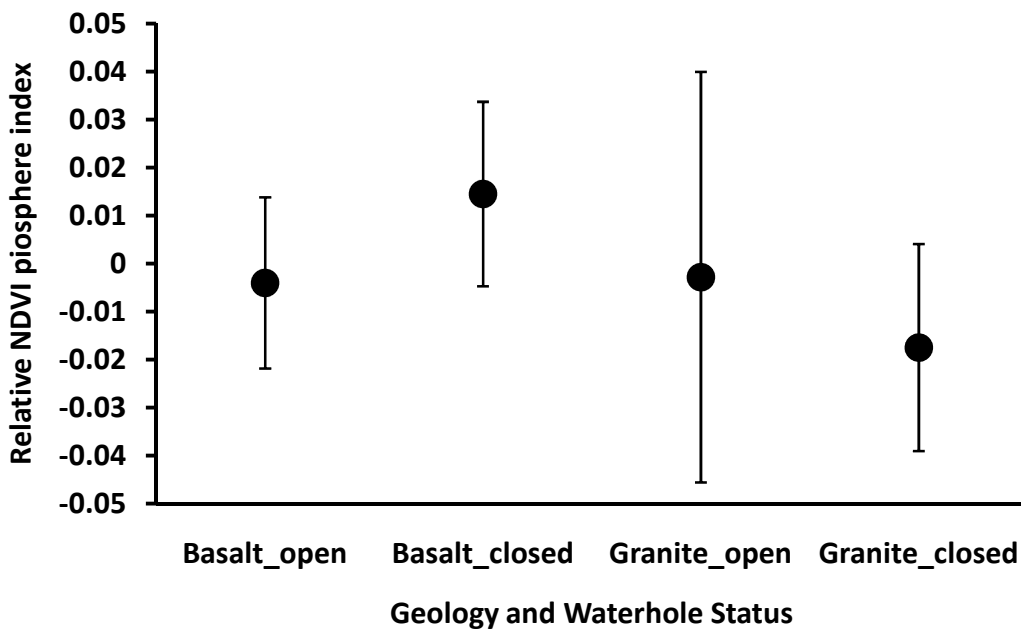


Fig.6.2. The effect of geology (granite vs. basalt) and waterhole status (open vs. closed) on the relative NDVI biosphere index. Dots represent mean values, vertical bars represent 95 % confidence intervals.

Table 6.2. The prevalence of different biosphere response patterns in 2000 and 2006

Response pattern	No. Sites (2000)	No sites (2006)
Positive linear	21	15

Remotely sensed piosphere gradients

Negative linear	11	10
Max. NDVI at intermediate distance	14	18
Min. NDVI at intermediate distance	12	15

6.4 DISCUSSION

Lind *et al.* (2003) studied the response of NDVI to distance from water at 44 boreholes in the rangelands of northern Senegal, and report that the piosphere pattern differed widely between sites. The most common pattern was an ‘inverse’ gradient, with high NDVI close to the waterhole and lower NDVI further from water, although the ‘normal’ piosphere pattern (low NDVI close to the waterhole and higher NDVI further away) was also common. They also report sites with composite patterns and sites lacking clear piosphere patterns. In our study, the most common response for both years was an increase in NDVI along the distance gradient (21 sites in 2000, 15 sites in 2006), although we also recorded some sites with the inverse pattern (11 sites in 2000, 10 sites in 2006), and other sites with minimum (12 sites in 2000, 15 sites in 2006) or maximum NDVI (14 sites in 2000, 18 sites in 2006) at intermediate distances from water. Lind *et al.* (2003) attribute the inverse piosphere pattern to nutrient inputs from dung and urine deposition close to waterholes. They note that this inverse pattern emerged particularly strongly in high rainfall years. In high rainfall years, productivity over the entire rangeland was high, but limited by the availability of nutrients (esp. phosphorus) in their study. High nutrient availability close to waterholes promotes a green flush, resulting in higher NDVI close to water than further away. We found no similar link between the inverse piosphere pattern and high rainfall – this piosphere pattern was equally common in 2000 (high rainfall) and 2006 (lower rainfall). This suggests that nutrient enrichment close to waterholes in wildlife systems such as the KNP is not as marked as in cattle systems, such as that studied by Lind *et al.* (2003). The more common ‘normal’ piosphere response (low NDVI close to water and higher NDVI further away) in our study is explained by lower vegetation biomass and cover closer to water than further away,

corresponding to high herbivore utilization pressure (grazing, browsing and trampling) close to water and low herbivore utilization further away, as has been found in other systems (Tolsma *et al.* 1987; Smet & Ward 2005).

One of the questions guiding this study was the usefulness of NDVI for monitoring piosphere dynamics at a large spatio-temporal scale. The clear piosphere gradients that emerged around many of the waterholes surveyed in the KNP indicate that NDVI is a suitable index of the effect of herbivore utilization on vegetation within the piosphere context, in sub-humid, perennial savanna. ***The Landsat images we used to derive NDVI are now freely available to researchers, minimising the fiscal constraints of ground-based piosphere surveys, and the resolution (30 X 30 m) of the satellite images was sufficient to detect a piosphere pattern. Unfortunately, clear (cloud-free) Landsat images from the late growing season (March – May) in the KNP were not readily available, limiting the study to two time periods. The results of this study have to be interpreted cautiously, given the fact that the image from 2000 dated to early April, while that from 2006 dated to mid-May. The 2006 image was thus taken five weeks later in the growing season than that from 2000. The drying out of the soil which would likely have taken place during those five weeks would result in a rapid reduction in both evapo-transpiration and the leaf area index, both of which significantly affect readings in the NIR band, and thus NDVI. However, the use of a relative NDVI piosphere index in this study, rather than actual NDVI values, allowed the effect of waterhole closure to be assessed in spite of this constraint.

In the six years between our two study periods, no significant vegetation recovery occurred around closed waterholes. NDVI was higher in 2000 than in 2006 for all waterholes, regardless of status (open or closed). We expected this pattern (Chapters 3 – 5, this thesis), due to the higher rainfall in 2000, because NDVI responds positively to rainfall (Gurgel & Ferreira 2003), and because the image from 2006 (12 May) was taken 5 weeks later in the growing season than the image from 2000 (4 April), but we predicted that the decline in NDVI between years would be lower at closed sites compared to open sites. The lack of difference in the relative NDVI piosphere index between open and closed sites suggests two possible scenarios: 1) vegetation gradients around waterholes recover slowly and sufficient time has not passed for significant recovery to have occurred and/or 2) vegetation resilience has been permanently compromised by artificial water provision. Large significant increases in herbaceous basal cover

and soil infiltration rates (ground-based surveys) recorded between the early 1990s (Thrash 1993) and the current study period (Chapters 3 – 5, this thesis), regardless of distance from water or waterhole status, suggest that neither vegetation nor soil resilience have been permanently affected by water provision.

We also found no significant effects of underlying geology and long-term growing conditions (MAP) on the relative NDVI piosphere index used in this study (i.e. the change in the piosphere gradient over time), although NDVI itself was weakly but significantly correlated with long-term MAP and was higher for vegetation on basalt-derived soils than on granite-derived soils. We expected that the higher nutrient status of basaltic soils would benefit recovering vegetation around closed waterholes, resulting in higher productivity and a greener flush (resulting in a more positive NDVI) around these sites compared to similar sites on the granites, and that the long-term growing conditions as determined by rainfall should also influence recovery. When using a composite NDVI value for each site, removing the effect of distance and time, neither geology nor long-term MAP proved significant. Thus, the size of the decline in NDVI that occurred between 2000 (high rainfall) and 2006 (low rainfall) was not dictated by geology (and thus by soil nutrient status) or long-term growing conditions. This result suggests that future vegetation recovery patterns around closed waterholes should be similar on both landscapes in the KNP (granitic and basaltic) and similar in regions with different rainfall.

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CHAPTER 7: CONCLUSIONS

Waterhole closure in the KNP has not resulted in significant vegetation and soil recovery after six years. Herbaceous basal cover and soil water infiltration capacity both increased significantly between 1990, when all the waterholes in this study were open, and 2006, when several sites were closed, regardless of waterhole status. In addition, clear zonal piospheres, well-described by the logistic regression equation, were recorded in 1990, but there were no clear piospheres for any soil or vegetation variables (except herbaceous species composition) in 2006. Such piosphere intermittency, which I hypothesize is linked to rainfall inputs between 2000 and 2006, coupled with increases of vegetative cover and soil water infiltration capacity, indicate that long-term artificial water provision in the KNP has not compromised vegetation and soil resilience or spatial heterogeneity in the long-term. Thus, I conclude that the potential for piosphere recovery remains intact, but takes place very slowly after waterhole closure.

The piosphere survey carried out in the early 1990s (Thrash 1993) took place at the end of a prolonged drought; the current study followed a period of above-average rainfall. I suggest that the status of the vegetation and soil in piosphere systems around open and closed sites in the KNP will only diverge following another prolonged dry period. I therefore recommend that piosphere monitoring continue into the future, because the efficacy of the waterhole closure policy can only be properly assessed after the next drought. Low herbivore densities and high abiotic heterogeneity in the KNP is also important to explain the weakness of the piosphere response in this study. Piospheres in sub-humid savanna ecosystems such as the KNP are intermittent and their existence is highly dependent on prevailing climatic conditions.

Since 1978, the logistic regression model has been commonly used to describe piosphere structure for any number of soil and vegetation parameters with increasing or decreasing responses to distance from water (Graetz & Ludwig 1978). This general piosphere model has been widely applied in a number of piosphere studies (Andrew 1988; Thrash 1993; Clegg 1999; Derry 2004). This model is fairly robust: manipulation of its parameters makes it highly adaptable to site-specific responses. The model's parameters are useful for the quantification of the piosphere zones predicted by the conceptual piosphere model. I found no general model of the response of a range of soil (texture, pH, organic matter, compaction, infiltration, total nitrogen and total phosphorus) and vegetation parameters (herbaceous basal cover and biomass)

to distance from water and the assumed grazing gradient around the sites surveyed in this study. Not only were there no consistent responses of particular variables across the eleven waterholes surveyed in the ground-based component of this study, but for individual sites, there were no consistent responses of different variables to distance from water. This is in agreement with comments by Thrash and Derry (1999), who in their review of piosphere literature note that the “range of responses found for vegetation and soil properties with distance from water across different study sites” is “antagonistic to any generalized piosphere modelling effort”. Only herbaceous species composition responded consistently to distance from water. Annual and disturbance-tolerant grass species and forbs dominated close to water at all sites and decreased in relative abundance with increasing distance from water, and perennial, disturbance-sensitive climax species had the opposite response. This pattern was consistent with the conceptual piosphere model, and suggests that herbivores are having a long-term, cumulative effect on vegetation around artificial waterholes in the KNP.

One of the most important conclusions to emerge from this study is the value of remote-sensing techniques for monitoring piosphere change at a landscape scale, using simple vegetation indices such as NDVI. The remote sensing component of this study supported the findings of the ground-based study – i.e. six years after waterhole closure there has been no significant vegetation recovery around closed waterholes. In addition, the ground-based, rapid assessment technique of Landscape Function Analysis (LFA), used to collect base-line data from around eleven waterholes in this study, is a suitable technique for future piosphere monitoring. This method of assessing the soil status (nutrient cycling, infiltration and resistance to erosion) avoids the cost of the laboratory tests used in this study to measure soil pH, nitrogen, phosphorus, organic matter and texture, and the time-consuming traditional methods of measuring infiltration and soil compaction. LFA also provides a reliable estimate of vegetative cover, without the necessity of measuring the basal cover of individual grass tufts.

To conclude, in this thesis I have shown that i) piospheres are an intermittent, climate-driven phenomenon in the KNP and ii) long-term artificial water provision in the KNP has not negatively affected vegetation and soil resilience. This result indicates that vegetation and soil recovery after waterhole closure is possible, although it takes place slowly.

7.1 REFERENCES

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