Rangeland degradation in the southern Kalahari

by

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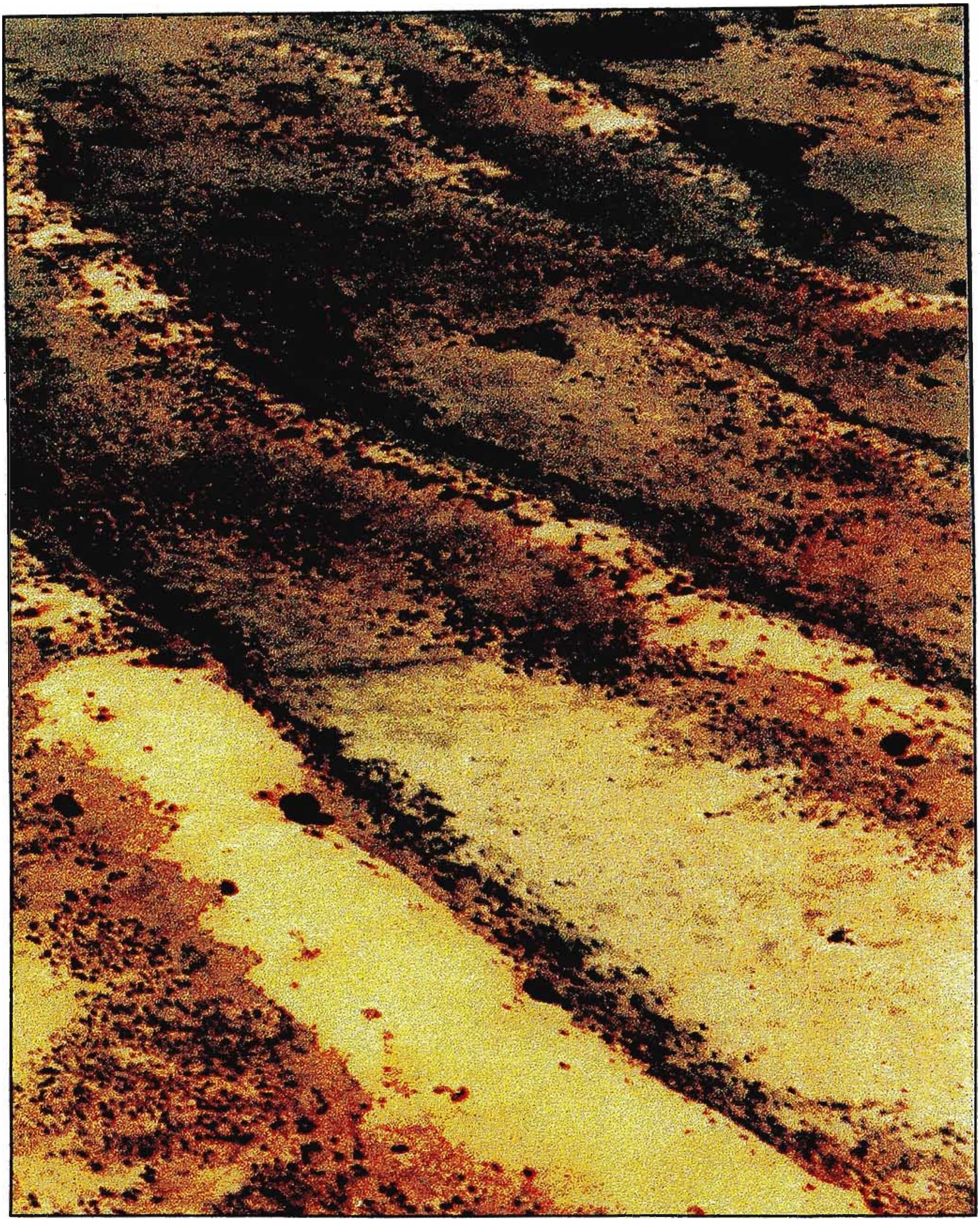
This thesis is dedicated to all the people
to whom the Kalahari is more than just a place on a map



FENCELINE CONTRAST COMMUNAL (bottom) & COMMERCIAL RANGELAND (top)

Abstract

Observations by local people in the Mier area, southern Kalahari, South Africa, indicated that degraded rangeland does not recover within a time frame acceptable to landowners.

Pristine vegetation in this linear dune system consists largely of a herbaceous layer dominated by perennial grasses. Woody vegetation is sparse on dunes and interdunes in good condition. The dunes and interdunes react differently to disturbance, probably because of differences in substrate stability, soil particle size distribution and consequent differences in soil nutrient distribution and moisture content. Degraded dunes are devoid of any vegetation, except for *Stipagrostis amabilis,* a rhizomatous grass which remain in small clumps, and the tree *Acacia haematoxylon.* The latter increases in numbers probably due to the high moisture content in degraded dunes. Moisture content in degraded dunes remain high even during prolonged dry periods. Interdunes are more susceptible to degradation and are invaded by the long-lived shrub *Rhigozum trichotomum* and the annual grass *Schmidtia kalahariensis.* Both these species compete with perennial grasses for moisture. Additionally, depleted seed banks and increased seed predation by ants (*Messor capensis)* may also affect the re-establishment of perennial grasses in the interdunes. The main conclusion from this study is that degraded southern Kalahari rangeland cannot recover spontaneously at the landscape scale because of a negative feedback mechanism that prevents establishment and growth of seedlings. The hypothesis put forward is that rangeland ceases to react to rainfall as an ecosystem driver as it becomes degraded. Once degraded, wind controls the dynamics of the system and recovery, irrespective of rainfall, is almost impossible. In contrast, detailed studies at the level of small isolated populations of *S. amabilis* and *S. ciliata* on degraded dunes indicate high rates of population growth. The scales at which these processes exist are contradictory and may not be contradicting. Rangeland managers should take cognisance of the influence of the spatial and temporal scale at which they operate, and on which they base their decisions.

Declaration:

I declare that this thesis is my own original work, except where otherwise stated in the text.

January 2000.

Acknowledgements

My sincere gratitude to Prof. Tim O'Connor for supervising this project. His frank and objective advice and criticism throughout the project greatly improved the work. He can, however, not be blamed for any errors or inconsistencies.

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Finally, I wish to express my greatest appreciation to my wife Claire, who suffered most from my frequent visits to the Kalahari. Also to my sons, Stephan, Martin and Emile, who so much enjoyed the times that we could spend together in the dunes, thank you for sharing this with me. Their continuous and unselfish encouragement and support made it easy to spend the many hours in the sun and behind the computer.

Table of contents

Chapter 1

Introduction:

Rangeland degradation in the southern Kalahari.

While human populations continue to increase because of improved living conditions and health standards, the pressure on natural resources continues to grow. Rangeland constitutes a major portion of the earth's surface, with some 1615 million ha world wide believed to be desertified (Mabbutt 1984). In Africa south of the Sudano-Sahel, an estimated 200 million ha (12% of the total) have been desertified (Mabbutt 1984). In South Africa, Hoffman *et al.* (1999) determined the extent of rangeland degradation on a magisterial district basis (sub-provincial authority), based on the experience and perceptions of experts in each district. Gordonia, the district which covers most of the southern Kalahari in South Africa, has been rated as having both soil and vegetation degradation values much higher than the country wide average. The methodology followed by Hoffman *et al.* (1999) does not allow for degradation estimates on a smaller scale, however, large areas of Gordonia are invaded by *Rhigozum trichotomum* (Moore 1989) and dunes in certain areas of Mier are bare (Leason 1996).

Extreme cases of rangeland degradation in the southern Kalahari are visually prominent in the Mier area. Dunes become completely bare with mobile sand, while the interdune areas are invaded by the shrub *Rhigozum trichotomum.* Primary productivity on both these habitats in the degraded state is very low (A. Stone unpubl.). However, it was not this initial unproductive state that concerned the people of Mier, but rather the inability of such rangeland to recover spontaneously once the agents of degradation have been removed, even during higher rainfall years. Local knowledge thus indicated that degraded Kalahari rangeland does not recover in a time scale relevant to the landowner.

The Clementsian succession model can not explain certain aspects of vegetation dynamics which suggests a predictable change towards, or away, from a climax vegetation composition. The inability of certain vegetation states to recover to former levels of productivity (or diversity or functionality), especially in the arid and semi-arid areas, can also not be explained by this model. These limitations of the Clementsian model have been central to the recent development of non-equilibrium models, such as: Westoby's *et al.* (1989) state-and-transition model; Friedel's (1991) concept of thresholds and Laycock's (1991) analogy of the cup and ball. Although these models were widely accepted, very little has been published on the underlying mechanisms that prevent or induce the changes portrayed within these models. Milton and Hoffman (1994) listed factors that may constrain natural vegetation recovery in degraded rangeland. These include both biotic factors (reduced seed banks, the existence of long lived unpalatable woody plants, loss of micro-symbionts etc) and abiotic factors (altered soil properties: reduced nutrients; reduced infiltration rates, and a reduction in the number of micro-sites that would trap seeds and provide safe sites for germination).

Friedel (1994) discussed how spatial and temporal scales affect the perception of change in rangelands. She indicated that, although states and transitions, and thresholds are valuable concepts, they are scale dependent, and their place in a spatial hierarchy needs redefining. The scale of operation is important, as it will not only influence our knowledge of how the system functions, but will also influence conclusions with regard to the results of monitoring actions. Investigations at the level of the individual plant or community may provide data that will lead to different conclusions than those drawn from a landscape wide study. Smaller scale investigations may be subjected to greater heterogeneity than larger scale investigations. On the other hand, studies at the larger scale may suffer from small scale heterogeneity being averaged away (Friedel 1994), reducing the resolution of study. Similarly, the time scale of investigation may have serious consequences for conclusions drawn from studies. Short-term studies may not include influences that are only expressed on the long term.

There is a need to investigate the processes and factors that prevent changes to more productive vegetation states in the southern Kalahari. In addition there is a need for this to be put into perspective of both spatial and temporal scales if effective management and restoration efforts such as the Kalahari LandCare Project is to succeed.

This thesis therefore focuses on rangeland degradation in the Mier rural area and attempts to unravel some of the links between the biotic and abiotic components of the southern Kalahari dune system. Van Rooyen (1998) described the larger project, of which this thesis forms a part, and its context within the new South Africa. The research objectives of this study are:

1. to describe rangeland degradation in the dune system of the southern Kalahari and the interaction between plant cover and ecosystem functioning;
2. to determine the role of moisture in the apparent inability of degraded rangeland to recover spontaneously;

3. to determine the extent of degradation using remotely sensed data;
4. to determine changes towards recovery at the micro-scale;
5. to provide information regarding the improvement of degraded areas in the study area.

Essentially there are three scales of investigation; the plant to sub-population scale (1 – 20 m^2); an intermediate level, which investigates ecological processes at the large patch scale (0.1 $\approx$10km^2) and the landscape scale (>10 km^2). The intermediate level of investigation can be regarded as more appropriate in terms of management, because it is this scale (both spatially and temporally) that the manager experiences and reacts to. The outer limits of investigation provide insight and information regarding the driving forces (smaller scale) and the net result of these impacts (large scale).

This study does not seek to provide all the answers regarding rangeland ecology in the southern Kalahari, but to highlight some important processes regarding degradation in the study area and to illustrate how this can facilitate the management of the natural resources in this largely unknown semi-arid environment.

Chapter 2

Study area: The Mier Rural Area.

Location

The study was conducted in the Mier Rural Area in the southern Kalahari, Northern Cape Province, South Africa. Mier lies south of the Kalahari Gemsbok National Park (KGNP) and between the Namibian and Botswana borders, i.e. between 26° and 26° 40' south, and between 20° and 20° 40' east (Figure 2.1).

Climate

Rainfall is low; median rainfall at Rietfontein is 146 mm per annum (mean of 80 years) with a coefficient of variation of 54.5% (Figure 2.2a). The rain falls predominantly during the summer months between January and April, when ambient temperatures and evaporative water losses are high (Figure 2.2b). Summer temperatures at Twee Rivieren are hot with average minimum and maximum temperatures above 15 and 30°C during the period November to March. Average minimum temperatures during the winter months are low, averaging below 5°C, but often falling below zero. Daytime temperatures during winter are mild (Figure 2.3). Absolute minimum and maximum for the period 1960 – 1994 were –10.3 and 45.4°C respectively.

Evolution and Characteristics of the Kalahari

The evolution and characteristics of the Kalahari have been described in detail by David

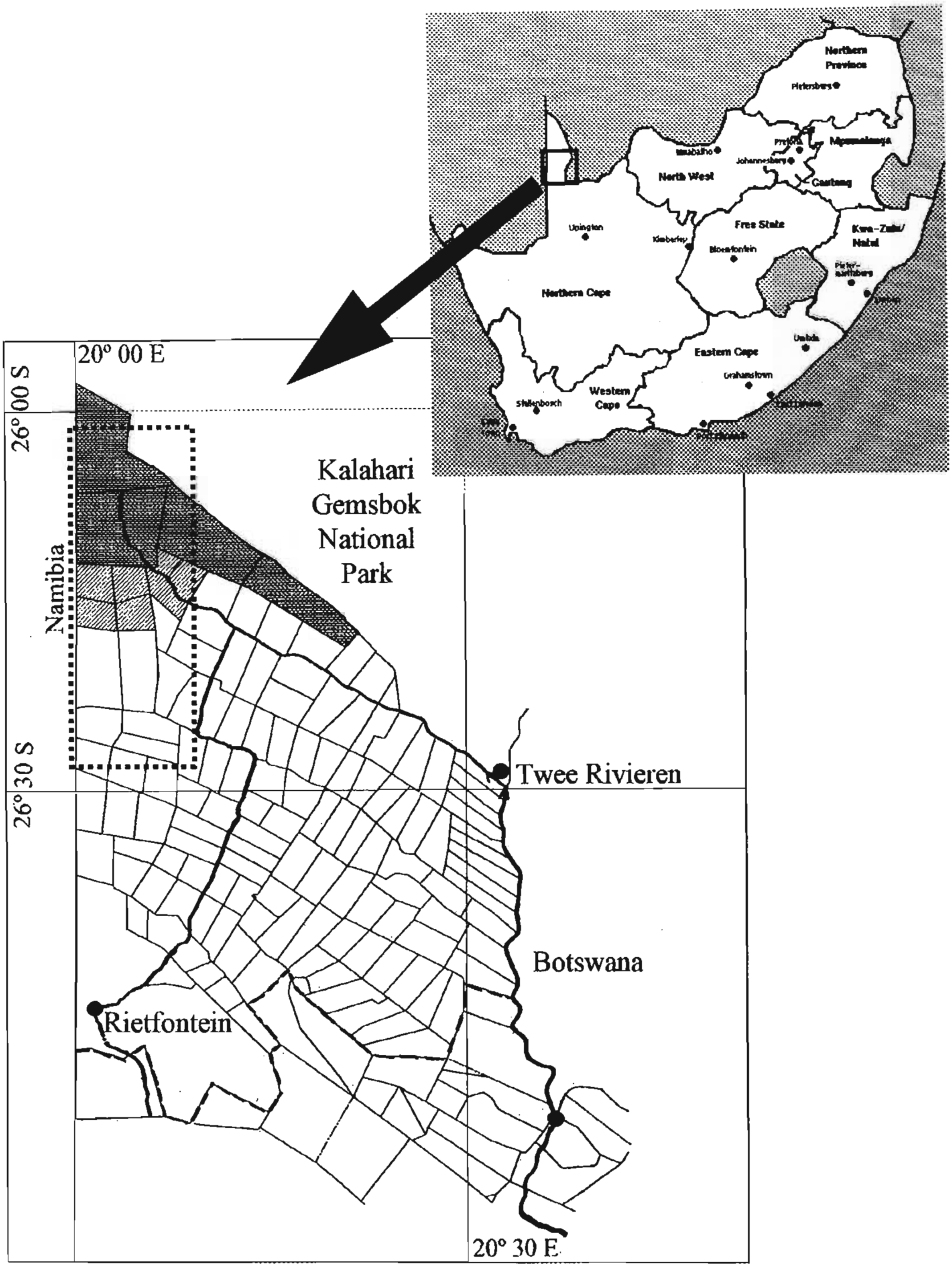


Figure 2.1 The Mier rural area. The shaded areas enclose the 'on-ground' study area, while the dotted line encloses the area studied with the use of remotely sensed data (Chapter 5). The darkly shaded areas are game ranches, while the hatched areas were the domestic stock ranches included in the study, the thin and thick solid lines indicate fences and gravel roads respectively.

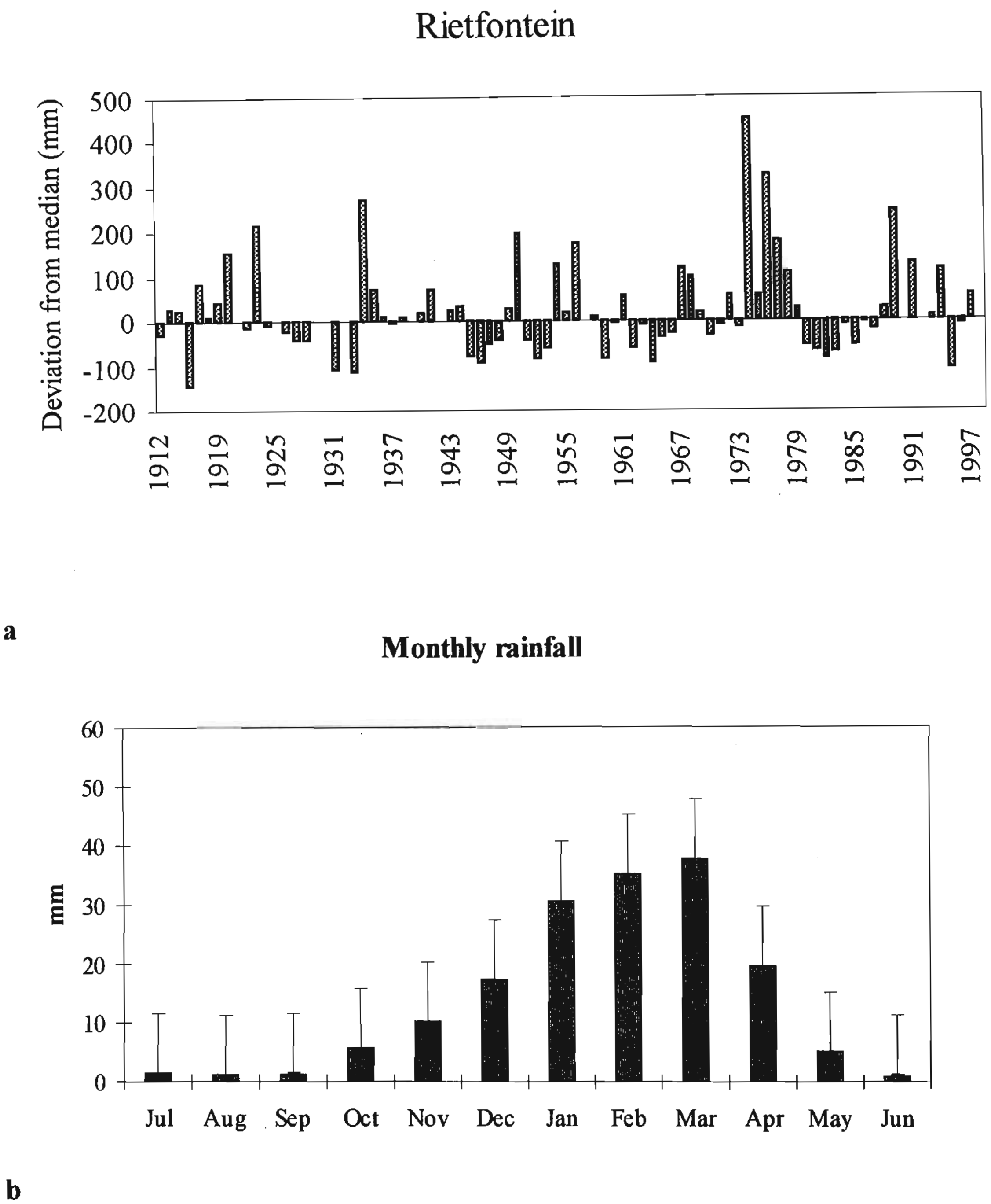


Figure 2.2 The rainfall at Rietfontein, in the Mier area. (a) Annual deviation from the median rainfall of 143.1mm. (b) Average monthly rainfall at Rietfontein. Vertical bars indicate 95% confidence intervals.

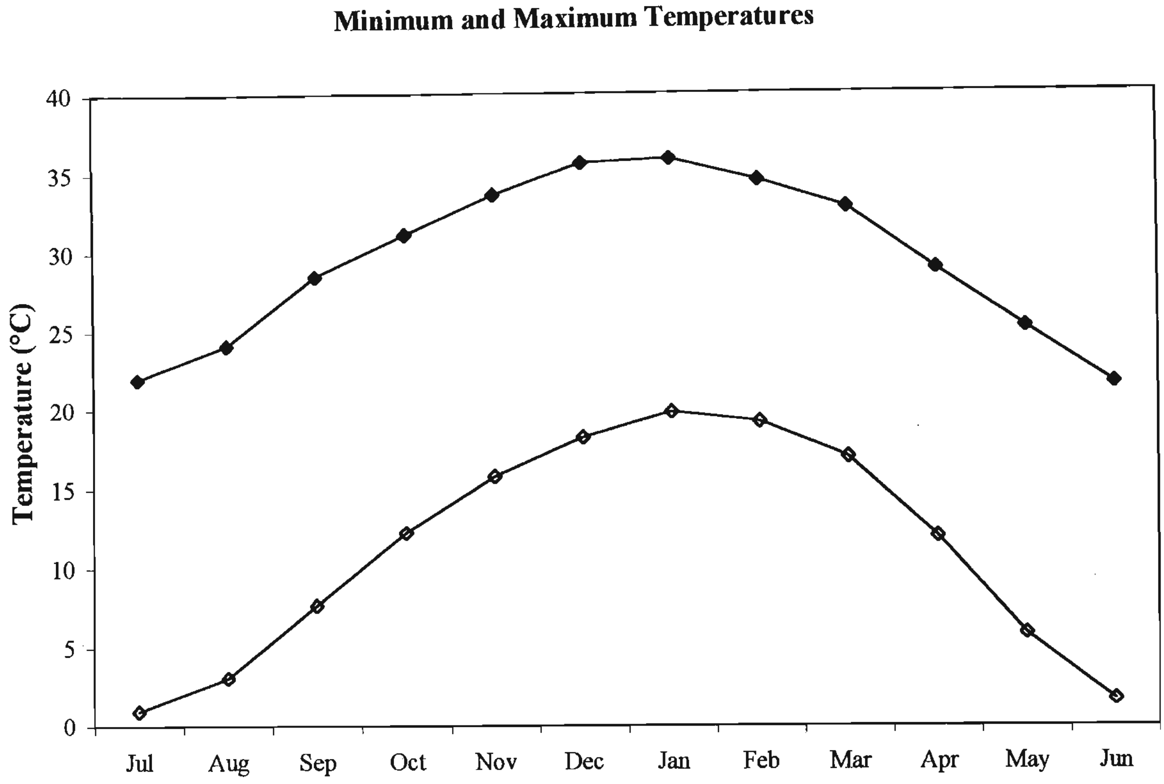


Figure 2.3 The average monthly minimum and maximum temperatures measured at Twee Rivieren, approximately 80 km south-east of the study area, for the period 1960 to 1994. Absolute minimum and maximum were –10.3 and 45.4°C respectively.

Thomas and co-workers (Thomas 1987, 1988; Thomas and Shaw 1988, 1990, 1991a, 1991b, 1993). According to Thomas and Shaw (1993) the name, Kalahari, refers to a structural basin, a group of sediments and an ill-defined desert region, which are intimately linked but also posses distinct characteristics. Structurally the Mega Kalahari occupies a series of contiguous Phanerozoic sedimentary basins; the Congo basin, the Cubango/Barotse basin and the Kalahari basin. The oldest sediments in the southern Kalahari basin are Permo-Carboniferous. The cretaceous and more recent sediments that have accumulated in this basin are collectively known as the Kalahari Groups (SACS, 1980) and vary in thickness from a few meters to more than 300m in northern Namibia. Environmental changes played a major role in the evolution of the Kalahari and distinguishing the differential influence of climatic changes from that of exogenic factors is crucial in developing a full understanding of the evolution of the Kalahari (Thomas and Shaw 1993). These sediments are capped by the surface sands, thought to be aeolian in character (Baillieul 1975).

Today the Kalahari constitutes roughly the area south of an imaginary line between the Etosha pan, in Namibia, to and including the Okavango delta, and as far south as the Orange river in the Northern Cape Province. Thus, extending over more than ten degrees of latitude, it possesses a highly variable climate and strong north to south-west rainfall gradient, 800 (in the north) to 150 mm (in the SW). Rainfall variability also increases to the south-west. The relief is low, and most of the Kalahari is at approximately 1000 m above sea level. Probably the most important characteristic of the Kalahari is the sand, as it is the most extensive sand sea on earth. Unconsolidated sand covers an area of 2.5 million km^2 in the Mega Kalahari.

The dune system

Since Grove's work published in 1969, the Kalahari has been the focus of Quarternary palaeo-environmental studies. The palaeo-environment in the Kalahari has been summarised by Deacon and Lancaster (1988). The sands of the Kalahari were blown into linear dunes which were subsequently fixed by savanna vegetation. Consequently the Kalahari is one of the most impressive pieces of evidence of the widespread nature of late Quarternary climatic changes (Deacon & Lancaster 1988). Three different dune subsystems occur in the Kalahari and are arranged in a semi-circular arc with a radius of some 1000 km. This arc corresponds approximately with the out blowing winds from the Southern African anticyclone situated over the Northern Province, SA. The northern dunes are situated around the Okavango Delta, the second subsystem is situated in western Zimbabwe and the adjacent parts of Botswana, while the north-north-west to south-south-east trending parallel dunes east of the Namibian highlands and north of the Orange River are the best developed dunes in the system. These dunes are 5 - 15 meters high with a spacing of 200 - 400 m, with their slip faces facing the south-west. The dunes resemble those found in the Simpson desert of Australia (Buckley 1981). Lancaster (1981) compared the distribution of active dunes with the 150 mm isohyet, and concluded that this is the rainfall threshold below which dunes are active. He concluded that the 150 mm isohyet must have been 1000-1200 km to the north-east when the northern dune system was formed. Sand mobility is, however, a function of wind intensity and vegetation cover, and various such relationships were devised (Talbot 1984; Ash and Wasson 1983, Lancaster 1987). The southern Kalahari dunefields were potentially active in the period 20 000 - 17 000 BP (Lancaster 1987). It has been estimated that temperatures during this time were some 5°C colder (Heaton *et al.* 1986), but wind speeds may have been 117 percent of present values (Newel *et al.* 1981). Deacon and Lancaster (1988) argue that these conditions may have rendered the dunes in the area active. The dunes in the study area were in existence prior to 33 000 - 28 000 BP when they were stabilised. These dunes, however, experienced several periods of activity and Lancaster (1978, 1987) recognised aeolian activity 20 000 - 17 000 BP, 12 000 - 9 000 BP, and again in the mid-Holocene.

Bullard *et al.* (1995) classified the dunes of the southern Kalahari according to morphological characteristics. The dunes in the study area fall within class two and three of this classification (i.e. the best developed linear dunes in the southern Kalahari). Wiggs and co-workers (Wiggs *et al.* 1994, 1995, 1996) reported on the effect of vegetation cover on airflow patterns across dunes and subsequent dune mobility. Although vegetation cover is the most important factor determining sand mobility (Wiggs *et al.* 1994), Wiggs *et al.* (1995) did not find a threshold vegetation cover beyond which the dune become active, but rather a gradient of activity. Within this gradient of activity, vegetation cover of less than 14% resulted in larger increases in sand mobility.

Lancaster (1986) reported on the grain-size characteristics of the dunes in the southern Kalahari and illustrated that grain size becomes larger, is better sorted and is more finely skewed from the interdune to the crest. He explained these factors in terms of the two ways in which sand moves across the surface when driven by wind, i.e. creep and saltation. In another study, albeit not in the same area but in the nearby Namib, which is of importance in this study (and also considered by Wiggs *et al.* 1995) is the increase of wind speed as it blows across a dune. Dune height and the direction are the main determinants of the specific speed-up factor for an area. The significance of this with regard to this study is that wind speeds at the dune crest are significantly higher than at the lower slopes or interdunes.

Soils and soil chemistry

The soils of the KGNP were described by van Rooyen (1984) and the relevant information is summarised. Of importance in this study is that only soils of Hutton (MacVicar *et al.* 1977) form are found in the dunes. The pans within the area consist mainly of the Swartland form.

The Hutton soils are characteristically red, with very weak horizon development. The B-horizon is also red and is structureless. These soils are generally in excess of 2 m deep. The parent material of these soils is mainly aeolian sand, with the iron oxide coated quartz grains comprising the major constituent (95%). Leistner (1967) divided the soils into various colours ranging from white to red. The sand overlays calcrete (a geological formation rather than a soil). Top soil is slightly acidic (pH 5-6) and lower layers are slightly alkaline (pH 7-8). Infiltration and water retaining capacities of these sandy soils are very high. Silt and clay portions vary between 1-2 and 1-5 % respectively (Leistner 1967).

The soils of the Kalahari are inherently infertile. Nitrogen is largely confined to the organic matter fraction. The sands of the Kalahari are also notoriously low in phosphates, which have often resulted in bovine parabotulism, a contagious disease amongst cattle as a result of eating bones in response to phosphate deficiency.

There is a general increase in total soil nitrogen going from the dune crest to the interdune with the surface layers having consistently higher total nitrogen levels than the deeper layers (Buckley *et al.* 1987). Phosphorus, Ca and K did not show the same catenal distribution as nitrogen, but P and K were also consistently higher on the surface than deeper whilst calcium concentrations were higher in the deeper layers (Buckley *et al.* 1987).

Vegetation

The vegetation in the Mier area is described as shrubby Kalahari dune bushveld (Van Rooyen & Bredenkamp 1996). Detailed vegetation descriptions of the vegetation of the southern Kalahari can be found in Leistner (1967) and Werger (1978), while most recent work regarding vegetation description and dynamics are confined to the Kalahari Gemsbok National Park (Van Rooyen, *et al.* 1984, Van Rooyen, *et al.* 1990, Van Rooyen, *et al.* 1991).

The vegetation of the southern Kalahari is generally determined by the area's topography.

Vegetation associated with the dunes and interdunes, pans and rivers are distinctly different (Leistner 1967, Van Rooyen, *et al.* 1991b).

The dominant grass species on dune crests is the perennial *Stipagrostis amabilis*, a hardy unpalatable clonal species. The annual grass, *Brachiaria glomerata* may be present in much lower densities. Various annual dicotyledons are common on dune crests: *Limeum* spp., *Gisekia* spp., *Hermbstaedtia glauca, Tribulus zeyheri, Citrullus lanatus* and *Hermannia* spp.. Woody species are essentially absent from the dune crests (Leistner 1967).

The vegetation on the dune slopes consists of *S. amabilis* on the upperslopes, followed by a band of *Centropodia glauca*, normally followed by *Stipagrostis ciliata* at the foot of the dune. Varying degrees of *Eragrostis lehmanniana* & *E. trichophora* and the forb species mentioned on the crest may also be found on the flanks. The woody species *Acacia haematoxylon, A. erioloba, Boscia albitrunca* and *Lycium* spp. occur in varying densities on the slopes.

Species composition in the interdunes depends on the soil depth. *Stipagrostis ciliata* and *C. glauca* dominate in deep red sands, while *S. obtusa* is common in shallow white sands. The dwarf shrub, *Monechma incanum*, often occurs on the transition between the interdune and dune areas, whilst *Rhigozum trichotomum* occurs in the interdunes.

Boreholes and piosheres.

Various authors reported on the effects of water points on rangeland condition in the Kalahari (Tolsma *et al.* 1987, Perkins and Thomas 1993, Dougill and Cox 1995). Most of the results of these studies are in agreement. However, the interpretation of the results differs remarkably. Typically these studies indicate increased nutrients in the immediate vicinity of water points as a result of livestock transporting nutrients centripetally towards the borehole from the surrounding savanna. Secondly, there is an increase in woody plants, referred to as the bush encroachment zone, in the area between approximately 100 to 2000 m from the borehole (this is obviously dependant on the 'age of the borehole' and the number of livestock utilising the borehole) (see Perkins and Thomas 1993, Dougill and Cox 1995). Tolsma *et al.* (1987) regard the changes in the nutrient balance as detrimental, while Perkins and Thomas (1993) are much more careful in judging the impact of boreholes, saying the impacts are not solely detrimental and suggest further long term monitoring. Doughill and Cox (1995) on the other hand are more bold and conclude (p19) " ... the ecological changes that have been brought about by grazing cannot be linked with the more fundamental changes in ecosystem function. Basic soil processes appear relatively unaffected by grazing pressure outside the sacrifice zone, and there is no evidence that the resilience of the system has been affected through soil degradation."

History of the Mier area

A group of so-called 'coloured people' moved from the Boland (Southern-western Cape) into the interior during the first part of the previous century, and settled in what is now known as the Mier area. In 1891 the British Crown annexed the land and incorporated it into British Bechuanaland, which later became part of the Cape Colony in terms of Act 41 of 1895. Many of the original occupiers lost their land rights at the beginning of the century allegedly by stealth and treachery. In 1930 the Coloured Persons Settlement Areas (Cape) Act was promulgated. It provided for the declaration of crown land reserved for the settlement of Coloured persons. The Mier settlement area fell under the Mission Stations and Communal

Reserves Act (Cape) of 1909 from the time Act 3 of 1961 came into operation. The preservation of Coloured Areas Act No 3 of 1961 made provision for the reservation by proclamation of land for occupation and ownership by Coloured persons and for land in an area so reserved to vest in the Minister in trust for the registered Coloured occupiers. In the course of years a process of individualisation of occupation of grazing areas occurred.

Mier today

The community now numbers between 4000 and 5000 individuals, many of whom live in the villages. The area comprises four land use types: towns and villages, communal grazing areas, commercialised stock farming by individual land "owners" and well managed communally owned game ranches. The 125 stock ranches range in extent from 1200 to 3500 ha. Sheep, goats and cattle are the most important livestock. Horses and donkeys are used only for transport.

The Mier community is highly dependent on agriculture for a living as the area holds no other natural resources, and business opportunities are extremely limited because of the remoteness of the area. Being a semi-desert, primary productivity of the land is very low, and very large areas are required for economically viable stock farming. This, together with population growth, has lead to a scarcity of land. The individual farms are generally too small for meat production beyond the level of "subsistence farming" and the commonages have become desertified through overgrazing.

Land tenure

The total Mier area comprises some 420 000 ha. 34000 ha is occupied by the villages (Rietfontein is the largest) and the communal grazing areas. Some 37 000 ha is managed as game ranches, and the rest (125 fenced ranches) are either leased from the Mier Transitional Legislative Council (TLC) or are individually owned. The game ranches are communally owned and the financial return from these areas is used by the TLC, in similar ways as other local authorities utilise taxes.

The previous government initiated a process whereby individual local farmers could buy the land and obtain title deeds. The land tenure issues are currently being addressed by the Minister of Agriculture and Land Affairs. In a recent report (Arendse *et al.* 1996) it is stated that the process whereby farmers acquired legal ownership of their farms was stopped and certain farms will be disowned and incorporated into the communal grazing areas. This will increase the existing communal grazing areas to some 45000 ha. The minister's report stipulates that management and monitoring plans should be instated for the communal areas. The other farms will again be available to be leased for periods of three years.

The Mier game camps

The core study area was in the game camps and stock farms in the immediate vicinity of these, while the remote sensing study was done on a larger area covering the game camps and a greater number of stock farms (Figure 2.1).

The South African Government has been involved in developing the Mier area since 1962 by establishing boreholes and fencing farms for sheep and cattle farming. As the area was developed from the south (see Figure 2.1), game species (predominantly springbok *Antidorcas marsupialis*, gemsbok *Oryx gazella* and eland *Taurotragus oryx*) which were still abundant in the area, moved north where large numbers concentrated on the southern boundary of the KGNP. During the late sixties, the then Southwest Africa border was fenced. The fence between the Kalahari Gemsbok National Park and the Mier area was completed in 1962/3 (van Wyk and Le Riche 1984). Although these fences were often broken by herds of large game species the game in the northern sections of the Mier area were effectively trapped. It was, however, not until 1978 that 'official' permission was given, by the old government Department of Coloured Affairs, to reduce the game in this area. It was then decided that these farms should remain "game farms" where hunting could take place. The farms Pulai/Lekkerdraai (14 454 ha), Loretta (6 405 ha), Twee 'n Dabas (10 466 ha) and Geisemab (6 448 ha) subsequently remained relatively undeveloped apart from fences, boreholes and a primitive road system. This proved to be a profitable practice for the community. These areas are managed by a subcommittee of the Mier TLC with assistance from the Northern Cape Department of Agriculture and the Agricultural Research Council: Range and Forage Institute.

The high concentration of game in this sensitive area caused extensive damage to the rangeland. *Rhigozum trichotomum* invaded the interdunes and the dunes crests were stripped of perennial grasses. The first scientific assessment of vegetation condition was done in 1985 by van Niekerk & de Wet (1985). Vegetation condition was poor for animal production, with few perennial species present. Carrying capacities for the different farms were set between 37 and 66 ha/LAU. Rangeland monitoring and the determination of carrying capacities continued and were done annually by the Department of Agriculture. Furthermore an attempt was made to manipulate animal numbers according to capacities set by the Department of Agriculture. Game censuses were done annually. There were no proper counts done before 1985 (Figure 2.4).

In an attempt to curb *R. trichotomum* invasion in the interdunes, certain areas were treated with chemical herbicides at great cost to the Mier TLC and the Department of Agriculture. Highly disturbed areas were fenced and withdrawn from utilisation. Although the killing of *R. trichotomum* was successful, there was very little improvement in the rangeland condition. Stands of *R. trichotomum* were replaced by monospecific stands of *Schmidtia kalahariensis*. This is a highly unpalatable species when actively growing because it produces volatile organic acids of very low pH (van Niekerk 1974). In one 4000 ha camp, excluded from grazing, virtually no recovery of vegetation took place during the last 8 years. Dune crests are still almost completely bare with sand movement preventing the re-establishment of grasses.

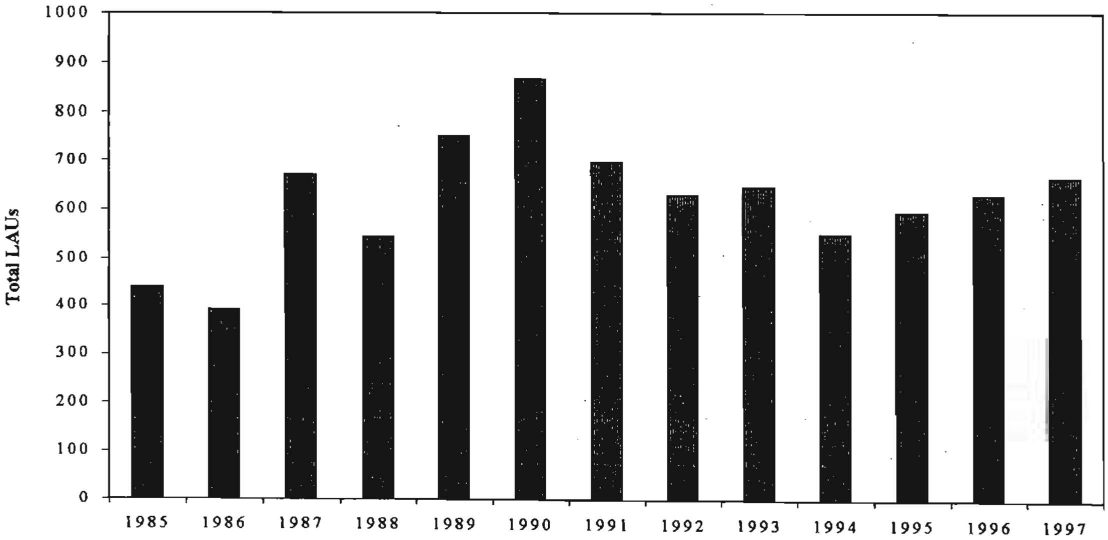


Figure 2.4 The total number of large animal units (LAU) present in all of the Mier game camps between 1985 and 1997. The size of the game camps was 44 172 ha until 1992 when it was reduced to 37 773 ha.

Chapter 3

Rangeland degradation in the southern Kalahari: positive feedback prevents natural recovery.

Introduction

Acocks (1953) suggested that the tufted nature and low cover of grasses, and the loose substrate make the southern Kalahari particularly vulnerable to disturbance. This notion was later supported by Leistner (1961) and other workers who confirmed the importance of vegetation cover on the stability of the dunes (Thomas 1992, Wiggs *et al.* 1995). In addition, Lancaster (1985) described the acceleration of wind from the dune's base to the crest, which increases the amount of potential sand movement towards the crest. Although it is clear that vegetation cover is an important factor preventing erosion (or surface instability) in the Kalahari, its role and interaction with other factors regarding rangeland degradation has not yet been quantified.

Local knowledge has it that degraded southern Kalahari rangeland does not recover, or at least not within a time period acceptable to the land user. This was also suggested by Bradshaw (1987) who hypothesised that degraded systems elsewhere may either remain stable, improve very slowly, or may degrade even further after the original disturbance has ceased. Various other models also support this notion; Friedel's (1991) concept of 'thresholds', the irreversible transitions in state-and-transition models (Westoby *et al.* 1989) and the domain of attraction or "cup and ball" models of Lewontin (1969) all suggest that certain states are stable and that any 'movement away' would require substantial external inputs.

A range of possible constraints on vegetation recovery after degradation in arid and semi-arid areas (Milton & Hoffman 1994) include: (i) a lack of seeds, (ii) the presence of long lived unpalatable woody plants; (iii) a reduction in micro-sites that would trap wind-blown seed and (iv) changes in habitat as a result of altered soil properties and micro-symbionts, compaction, reduced rainfall infiltration and increased exposure to sun, frost and wind. All these factors may singly, or in concert, prevent vegetation recovery. However, very little information regarding the interaction between these factors and their combined effect on ecosystem function is known.

Although certain aspects of the southern Kalahari ecology have been studied, including vegetation (Leistner 1967; Fourie *et al.* 1987; van Rooyen *et al.* 1990, 1991a, 1991b, 1994), nutrients (Buckley 1981; Buckley *et al.*1987a & b), wind velocity and sand movement (Lancaster 1985; Wiggs *et al.*1995) and soil particle sizes (Lancaster 1986; Buckley 1989), their relationships, interactions and subsequent influence on preventing natural recovery of vegetation after disturbance is largely unknown. The main aim of this study was to determine the biotic and environmental changes in ecosystem functioning during rangeland degradation that may constrain recovery to conditions with higher primary productivity. The specific objectives were to:

(i) describe a degradation gradient within the study area;

(ii) describe the changes in vegetation cover and species composition along the degradation gradient accounting for topography;

(iii) describe sand movement in relation to plant cover;

(iv) describe subsequent changes in the soil particle size distribution;

(vi) describe associated changes in the nutrient content of the soil.

Methods

Vegetation

Thirty-two sites were selected to include a wide variation in rangeland condition. The presence of fenced ranches (including both game and domestic stock of differing densities) allowed for 'fence-line comparisons'. These were done on the assumption that environmental variables were comparable on either side and only management (stock and game numbers) differed. Very shallow soils in the interdunes, i.e. white sand close to the calcrete layer with *Stipagrostis obtusa* the dominant plant species (Leistner 1967), were avoided because they made up only a small proportion of the study area.

Plant species and litter cover was ranked using an eight point scale (Walker 1976) in 30, 1m^2 quadrates on the each of the sub-habitats studied, i.e. dune crest, the opposite slopes (south-western and north-eastern), and in the adjacent southwestern interdune. Quadrates were placed six meters apart in two parallel transects along the length of the dune, in order to capture the variation in vegetation within the specific sub-habitat in an area of dune some 90 m long. Plant height was measured (per quadrate) to the level of the highest standing vegetative growth, thus excluding the higher growing inflorescences. Woody vegetation (cover and number of clumps) was measured in one 100 x 5m belt transect in each of the sub-habitats studied. Cover was measured as the average of the longest and shortest diameters of the clumps.

Framework of analysis and statistical procedures.

A multivariate approach was used to order sites along a gradient which could be interpreted according to previous management history and known environmental variables (Friedel *et al.* 1988). The first axis, where sites of obviously different range condition have been selected, may usually represent a degradation gradient (Bosch 1989). Principal components analysis (CANOCO; Ter Braak 1987a) was used to analyse herbaceous species cover data, because the most abundant species occurred in a linear fashion across the degradation gradient. As suggested by Ter Braak (1987b) species data was not standardised, to avoid the less abundant species dominating the ordination.

Although each site consisted of separate aspects, data from the dunes (slopes and crest) was first averaged to treat the dune as a single unit. Both dunes and interdunes were included in the first ordination analysis in order to examine the relationship between the dunes and interdunes. The dunes and interdunes were subsequently analysed separately, in order to prevent obvious differences in species composition and substrate over-riding the potential influence of rangeland condition on the ordination. The ordination axes were related to past and current management practices, and their influence on environmental variables (soil particle size, nutrients and sand movement) was tested using regression analysis. Data pertaining to the dunes only was analysed to investigate the relationship between the slopes and crest. Baseline values of these variables are given irrespective of rangeland condition in relation to topography of the area.

To simplify potentially cluttered graphs, species plots are not presented together with the samples plots (to produce the conventional bi-plot), but were printed separately (with the original axis scales as provided by CANOCO). Linear correlation was used to test the axes scores with other environmental variables.

Condition score

Rangeland condition was calculated following the procedure of Fourie *et al.* (1987). Calculations in the present study were however based on aerial cover and not on relative species composition as done by Fourie *et al.* (1987). The Fourie *et al.* (1987) method scores plant species according to their relative grazing value, which in turn is based on the plant's potential to produce dry matter, its palatability, nutritional value and potential to survive drought and grazing. Four categories are recognised: Group a: palatable plants with high nutritional value which decrease as a result of mild over utilisation, scored ten; group b: plants that increase during mild over utilisation which was scored 7; group c: unpalatable species that increase during heavy utilisation which scored 4; and group c: species with very little grazing value or invasive species which scored 1. It is assumed that this classification holds true for both domestic stock and the game species found in the area.

Past and Present impacts on vegetation

In order to relate present rangeland condition to potential causes of degradation, data regarding past and present grazing pressures on the ranches studied were collected from the relevant government bodies (Northern Cape Dept of Nature Conservation and Northern Cape Dept of Agriculture) and individual farmers. Additional information concerning other factors that can influence rangeland condition were collected: proximity to homesteads and water points, the duration of occupancy by subsistence farmers and the number of livestock owned by them.

To reduce the number of variables, all causal factors relating to grazing were scaled as either one, two or three, and then lumped into two groups, 'historical' 1970-1985 or current grazing pressures. Where grazing pressure was high, (in cases were animal numbers exceeded the current recommended stocking rate prescribed by the Northern Cape Department of Agriculture) grazing pressure was scored '3', '2' represented grazing pressure within reasonable limits of the recommended stocking rate, and '1' where animal numbers were lower than recommended. Other factors, such as the proximity of a site to homesteads or water points, or whether there was reasonable evidence of severe fires in the past were simply classes '1' or '0'. Sites close to water points in game ranches were awarded a zero for the 'proximity to water points', because the indigenous herbivores (especially springbok and gemsbok) in these areas are highly mobile and independent of water for most of the year.

Finally, a disturbance coefficient was calculated, which is the sum of the numeric classes allocated to each site above. For example, the disturbance coefficient of a site which experienced high grazing pressures in the past, and present, away from a water point which did not experience a major fire were calculated as follows: 3+3+0+0=6.

Climatological data

An automated weather station was established on one of the degraded sites (26° 11' 30" S & 20° 01' 25" E) in January 1995, at which temperature (daily minimum and maximum), humidity and wind direction was recorded on the dune, while wind velocity was recorded both on the dune crest and in the adjacent south-western interdune. Wind velocity was stored as an average wind speed per day measured in $m.s^{-1}$. A speed-up factor between interdune and dune crest was calculated following Mason & Sykes (1979).

Sand movement

Vertical movement of sand on dune crests and slopes was used as an indicator of surface stability. This was done using nine (1 m long, 6 mm diameter) metal stakes inserted to a known depth and arranged as a 3X3 grid, with stakes 3m apart. Stakes were placed on the crests and slopes of nine dunes investigated, interdune areas were excluded because of their relatively stable nature. This allowed vertical sand movement to be estimated by measuring the distance from the top of the stake to the level of the sand, at approximately monthly intervals between January 1995 and July 1997.

Soil particle size distribution and nutrients

Soil samples were collected on the crests, slopes and in the interdunes of each site: 20 soil samples were collected at five metre intervals along a 100m tape, from the top 5 cm soil layer and combined into one sample per sub-habitat. Particle size distribution was determined by sieving air dry soils through a nest of 12 sieves ranging in mesh aperture from 53-2000 μm using an automatic sieve shaker and weighing the mass of particles retained in each sieve.

Before nutrient analyses, soils were first air dried and sieved through a 2 mm sieve. Total soil nitrogen was measured by distillation and acid titration (Bremner 1965) following kjeldhal digestion. Total phosphorus was measured after digestion in concentrated HCl (Hesse 1971) and plant available phosphorus was determined in an ion-exchange resin extraction (Saggar *et al.* 1990). All phosphorus concentrations were measured colorimetrically using a molybdemum blue colour development (Murphy and Riley 1962). Soil pH was measured in a 0.001 M Ca2Cl solution and organic matter was determined by combustion at 450° C for 16 hours. Extractable K, Mg and Ca were measured on an atomic absorption spectrophotometer.

Results

Climatological data

Wind velocities were higher during the summer months, September to February, than during the colder months (Figure 3.1a). The average wind velocity measured on the dune (3.69m/s) was significantly higher than that recorded in the interdune (2.55) ($t=10.36$; $p<0.0001$) (Figure 3.1b). Daily speed-up factors varied between 0.92 and 3.74 with an average of 1.52. Dunes, and in particular dune crests are thus much more vulnerable to wind erosion than the lower slopes and interdunes, especially during the dry, windy months.

Vegetation

Dunes and interdunes

Eigen values of the four PCA axes of the combined data set (dunes and interdunes) were 0.645, 0.147, 0.05 and 0.04. The first two axes, which accounted for 79% of the variation, clearly separated the dunes from the interdunes in the PCA plot (Figure 3.2). This justified the use of only the first two axes because the dunes and interdunes were substantially different with regard to the substrate and species composition.

Furthermore, it is clear from Figure 3.2 that the first axis is a consequence of the variation in *S. kalahariensis* cover, while the other species contribute very little to this axis. Consequently the interdunes, where *S. kalahariensis* is the dominant species, were associated with the first PCA axis. In contrast to the first axis, *S. kalahariensis*' contribution to the strength of the second axis was much smaller, which was largely determined by species associated with the dunes, i.e. *Centropodia glauca*, *Brachiaria glomerata* and *Stipagrostis*

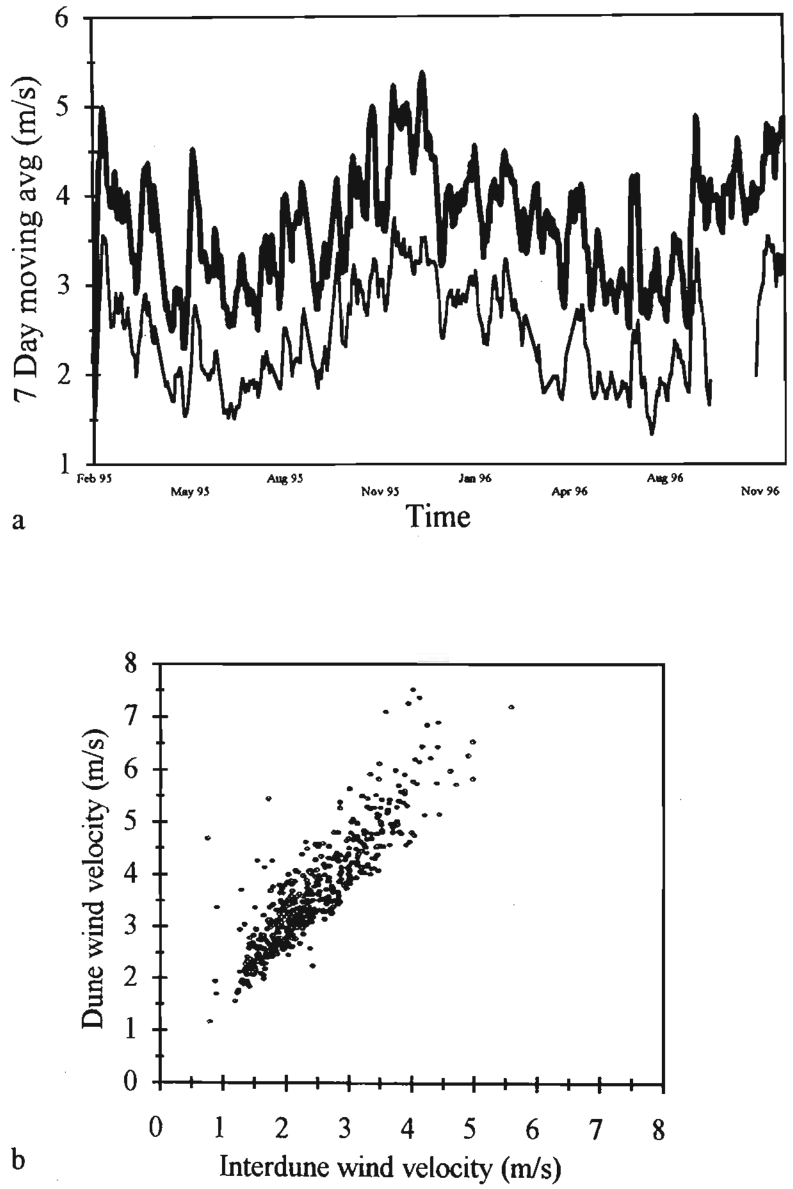


Figure 3.1 (a) The seven-day moving average of average daily wind velocity (m/s) on the dune crest (thick line) and in the adjacent south western interdune (thin line). (b) The relationship between the wind velocity in the interdune (x-axis) and the dune crest (y-axis).

amabilis. The approximately right angle of *S. kalahariensis* and the other species indicates that these species' distribution is essentially independent (Figure 3.2). The first two axes thus separated the dunes and interdunes dunes in the ordination space, which is confirmed by the positive correlations between the first and second PCA axis and the plant cover on the interdune and dunes respectively (herbaceous cover in interdunes vs. axis 1: $r=0.86$; $p<0.001$, herbaceous cover on dunes vs. axis 2: $r=0.92$; $p<0.0001$). This separation between dunes and interdunes, together with the clearly independent species associated with the dunes and interdunes, provided a basis for the subsequent separate analysis of the dune and interdune data. The host of species near the origin had a minor influence on the ordination either because of very low cover values or because of their infrequent occurrence.

Interdunes

The first axis of the ordination of the interdune data accounted for 99% of the variation while eigen values for the other three axes were 0.005, 0.002 and 0.002 respectively. The main axis of variation is simply a consequence of the cover of *S. kalahariensis* (Figure 3.3a). Although the second axis does not contribute much to the overall ordination, it is determined by the variation of *C. glauca*, *Hermannia tomentosa*, *Eragrostis lehmanniana* and *Stipagrostis uniplumis*. The first axis was correlated well with the total vegetation cover ($r=0.940$), *S. kalahariensis* ($r=0.999$) and the condition score ($r=0.731$), but not with disturbance coefficient or any of its components.

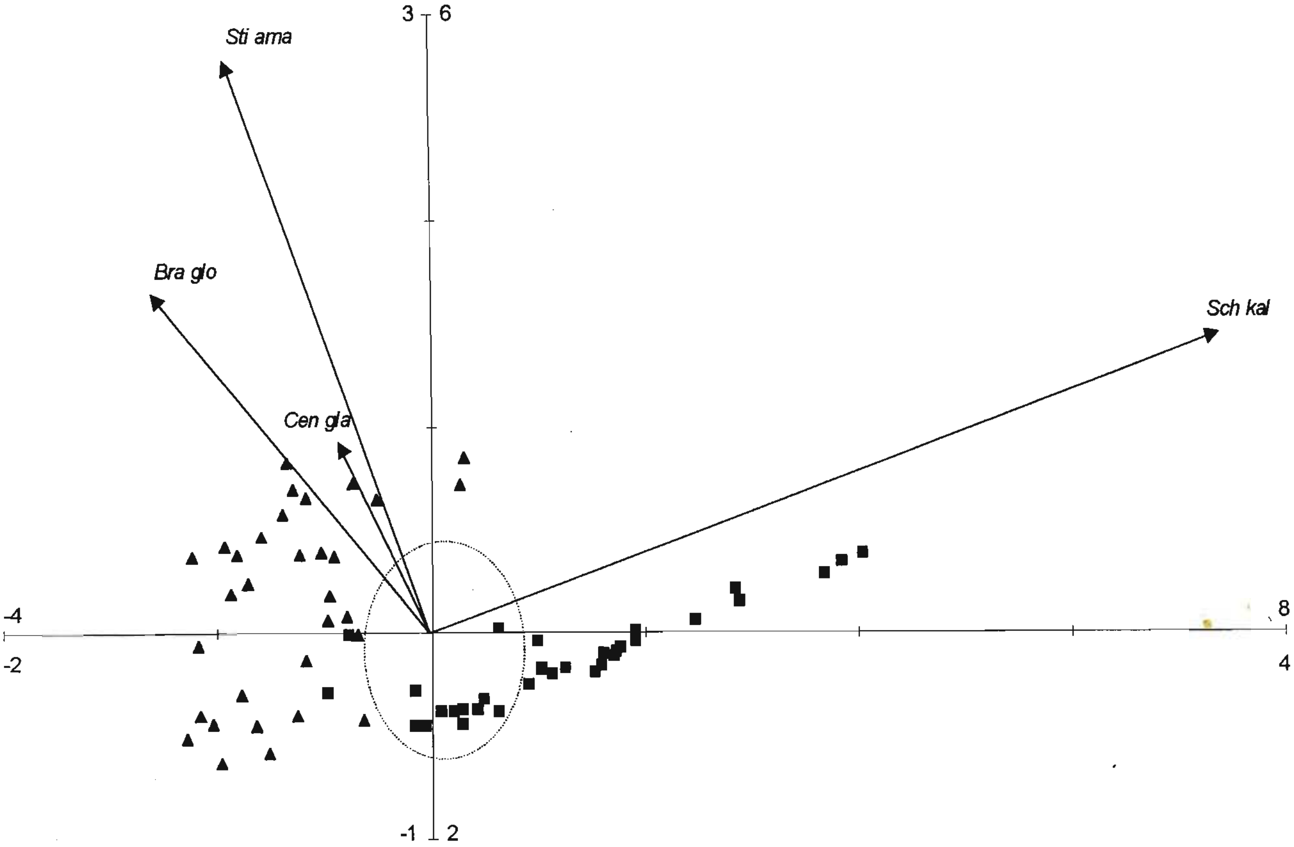


Figure 3.2 A plot of the sites (dunes: ▲, interdunes: ■) and species (arrows) in relation to the first two axes of the PCA of the complete data set. The ellipse on the origin of the species plot encapsulates several other species. The scale above the first and to the right of the second axis applies to the species and the other to the sites. Key to the grass species: *Sti ama, Stipagrostis amabilis; Bra glo, Brachiaria glomerata; Cen gla, Centropodia glauca, Sch kal, Schmidtia kalahariensis;* the other species are: *Eragrostis lehmanniana, Stipagrostis uniplumis, Senicio burchellii, Indigofera daleoides, Hermannia tomentosa, Limeum arenicolum, Limeum fenestratum, Hermbstaedtia glauca, Melolobium macrocalyx, Acanthosicyos naudinianus, Citrullus lanatus, Gisekia africana, Stipagrostis ciliata, Crotolaria spartoides, Sesamum triphyllum, Tribulus zeyheri, Oxygonum delagoense, Crotalaria africana, Protasparagus nelsii, Limeum* spp, *Hermannia* spp, *Aptosimum procumbens, Aristida meridionalis.*

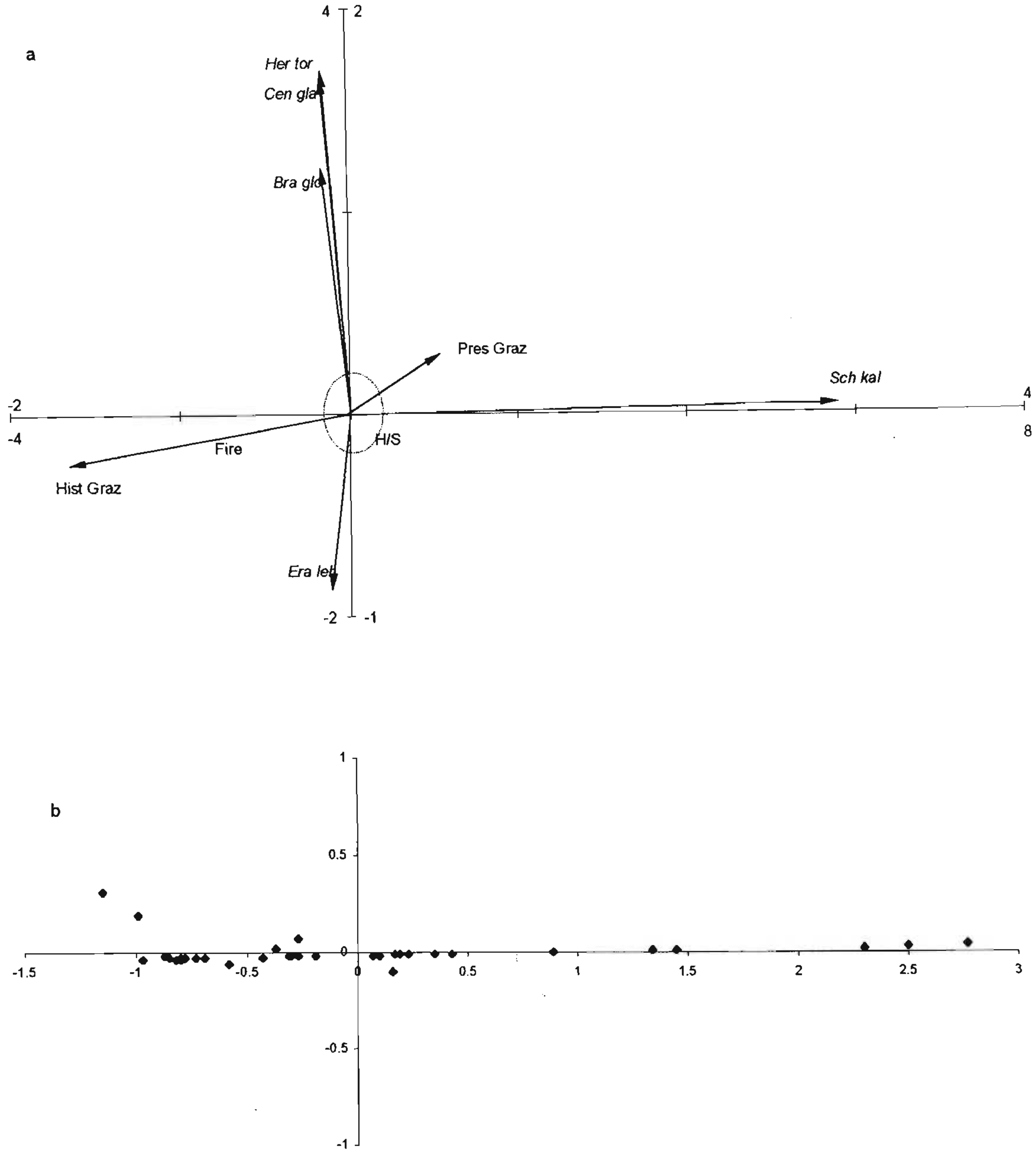


Figure 3.3 (a) A plot of species and environmental variables (arrows) and (b) sites in relation to the first two axis of the PCA of the interdune data only. The ellipse on the origin of the species plot encapsulates several other species. The scale above the first and to the right of the second axis applies to the environmental variables. Pres Graz, His Graz, H/S and Fire refer the environmental variables: present grazing pressure, historical grazing pressure, proximity to homesteads and fire. Key to the grass species: *Cen gla, Centropodia glauca; Bra glo, Brachiaria glomerata; Her tor, Hermannia tomentosa; Sch kal, Schmidtia kalahariensis*; the other species are *Stipagrostis uniplumis, Tribulus zeyheri, Stipagrostis ciliata, Aptosimum procumbens, Acanthosicyos naudinianus, Citrullus lanatus, Eragrostis lehmanniana, Indigofera daleoides, Hermbstaedtia glauca, Melolobium macrocalyx, Crotalaria spartoides, Oxygonum delagoenses, Sesamum triphyllum, Convolvulus sagittatus, Stipagrostis obtusa, Gisekia africana.*

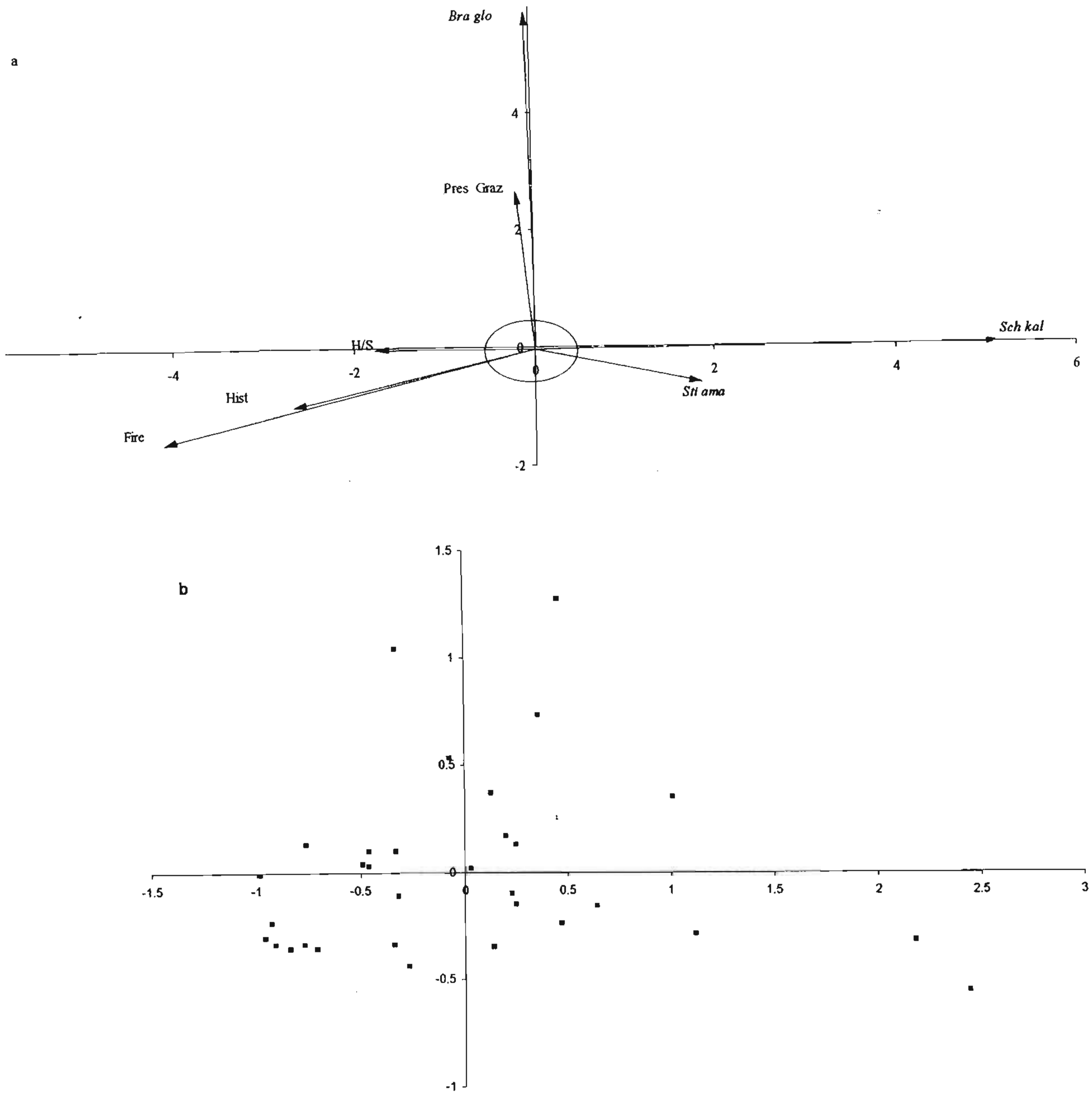


Figure 3.4 (a) A plot of species and environmental variables (arrows) and (b) sites in relation to the first two axis of the PCA of the dune data only. The ellipse on the origin of the species plot encapsulates several other species. The scale above the first and to the right of the second axis applies to the environmental variables. Pres Graz, His Graz, H/S and Fire refer the environmental variables: present grazing pressure, historical grazing pressure, proximity to homesteads and fire respectively. Key to the grass species: *Bra glo, Brachiaria glomerata; Sti ama, Stipagrostis amabilis; Sch kal, Schmidtia kalahariensis*; the other species are *Centropodia glauca, Eragrostis lehmanniana, Stipagrostis uniplumis, Senecio burchellii, Indigofera daleoides, Hermannia tomentosa, Limeum arenicolum, Limeum fenestratum, Hermbstaedtia glauca, Melolobium macrocalyx, Acanthosicyos naudinianus, Citrullus lanatus, Gisekia africana, Stipagrostis ciliata, Crotolaria spartoides, Sesamum triphyllum, Tribulus zeyheri, Oxygonum delagoense, Crotalaria africana, Protasparagus nelsii, Limeum* spp, *Hermannia* spp, *Aptosimum procumbens, Aristida meridionalis.*

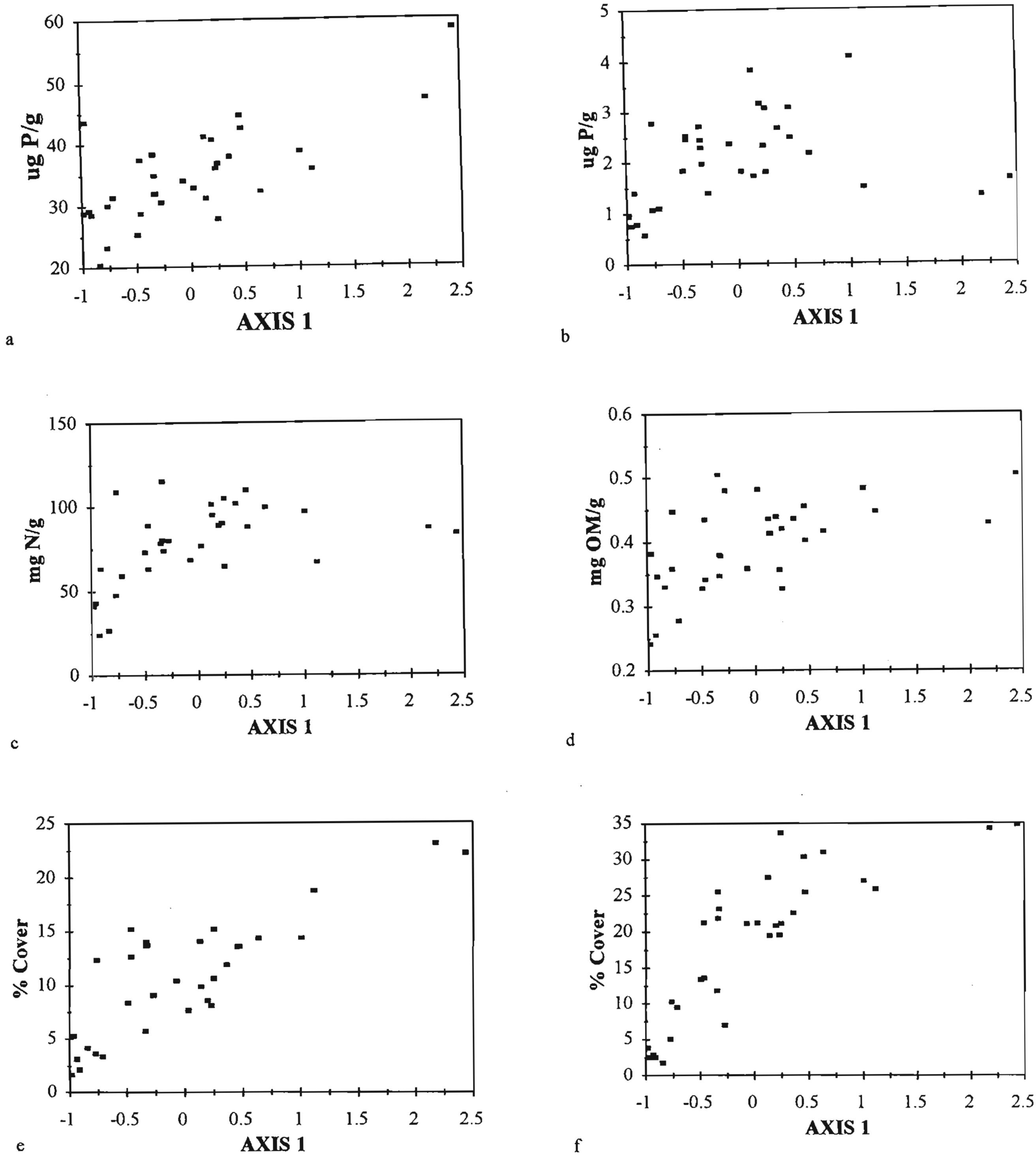


Figure 3.5 The relationship between important nutrients (a) total phosphorus, (b) available phosphorus, (c) total nitrogen, (d) organic matter, (e) plant litter and (f) total herbaceous plant cover with the first PCA axis of the combined dune data. r-Values and statistical significance are indicated in Table 3.1.

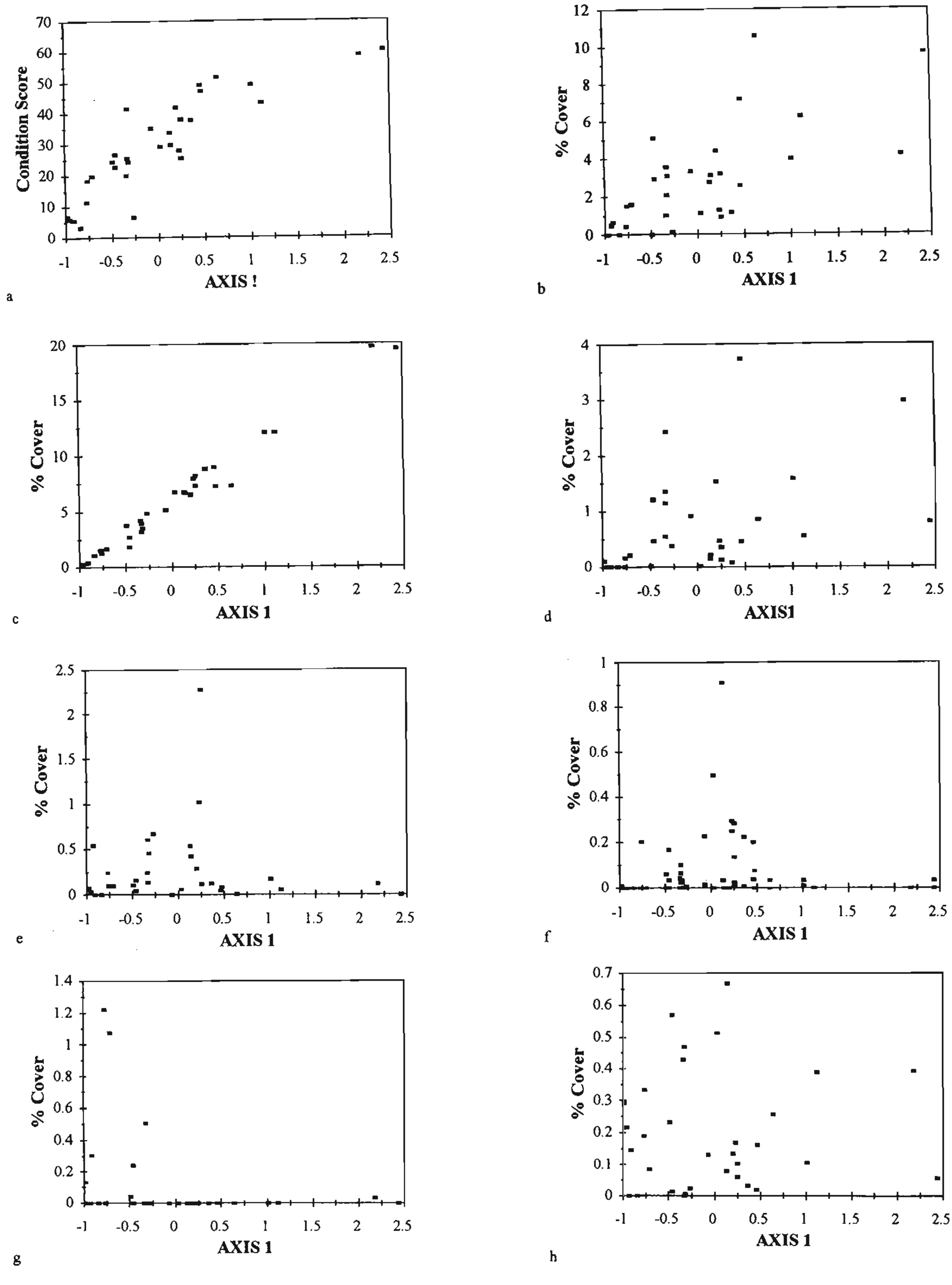


Figure 3.6 The relationship between the first PCA axis for the combined dune data and (a) condition score (based on important herbaceous species), (b) *Stipagrostis amabilis* (c) *Schmidtia kalahariensis* (d) *Centropodia glauca* (e) *Eragrostis lehmanniana* (f) *Acanthosicyos naudinianus* and *Citrullus lanatus* (g) *Hermannia tomentosa* (h) and *Limeum arenicolum*. r-Values and statistical significance are indicated in Table 3.1, those not listed were not significant.

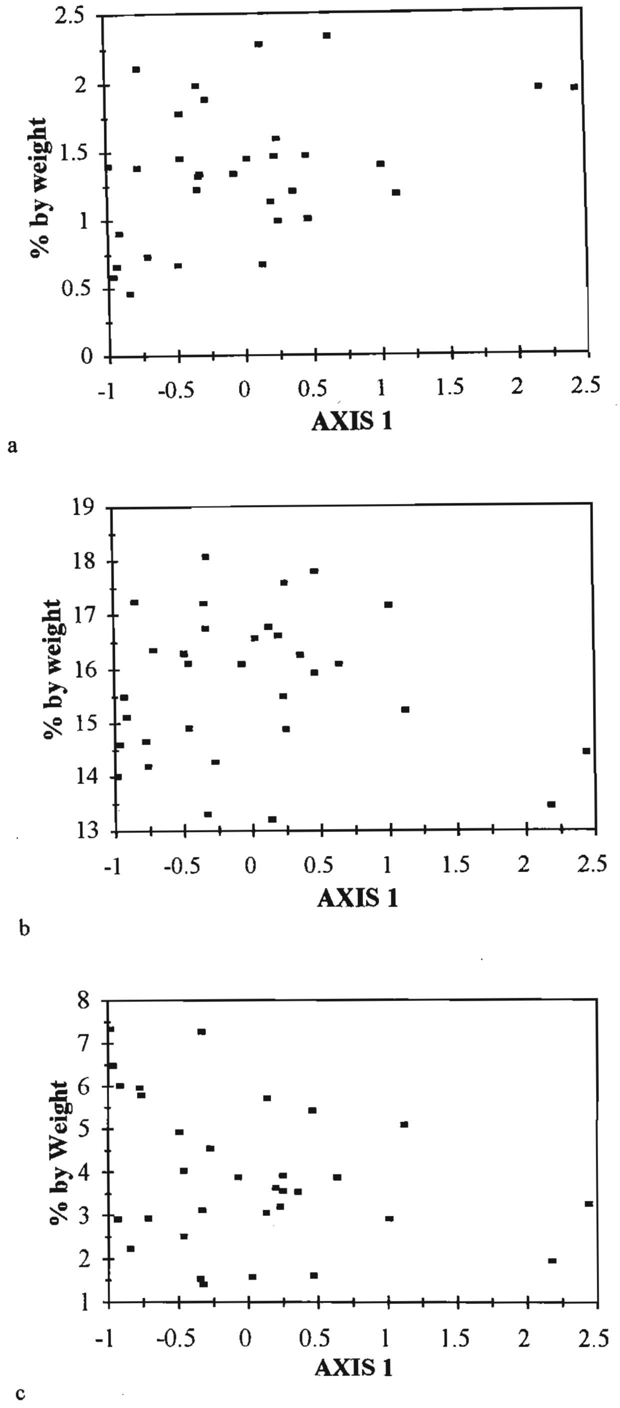


Figure 3.7 The relationship between (a) small: >53μ; r=0.43, p<0.05), (b) medium: not significant) and (c) large grain sizes: >425μ; not significant, in relation to the first PCA axis of the combined dune data.

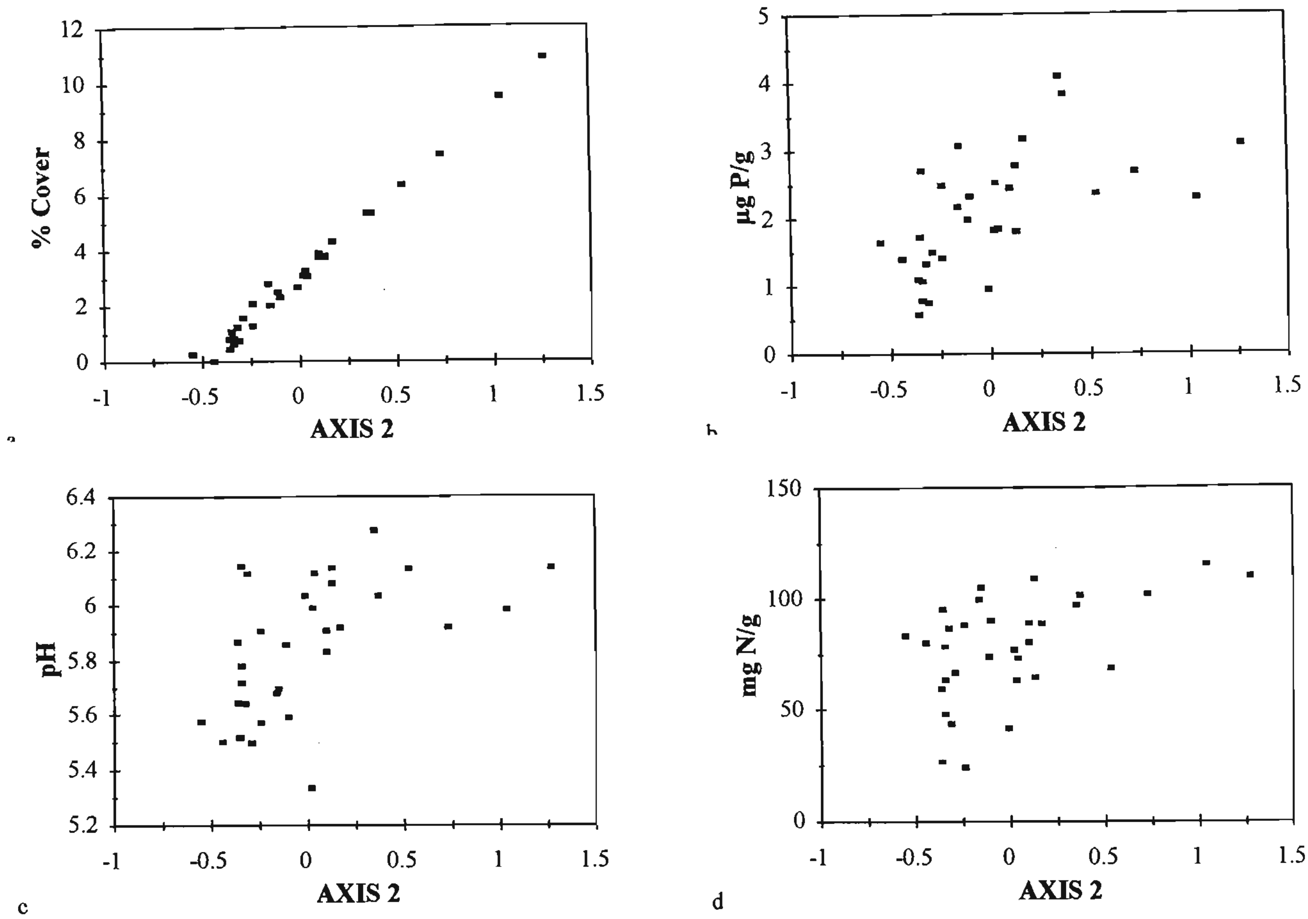


Figure 3.8 The relationship between the second PCA axis of the combined dune data and (a) the cover of *B. glomerata*, (b) available phosphorous, (c) pH and (d) total nitrogen. All four relationships are significant, refer to Table 3.2 for r-values.

Dunes combined

The eigen values of the first two axis were 0.666 and 0.173, while the third and fourth axis accounted for only 11.2% and 1.5% of the variation. Although the third axis could contribute to the ordination it was not included because the main focus of this investigation was covered by the first two axes. The first axis (Figure 3.4a) was strongly related to *S. kalahariensis* and *S. amabilis* cover while *B. glomerata* cover dominated the second axis. In contrast to the interdune, the dominant perennial species on the dunes *S. amabilis,* was well correlated with the *S. kalahariensis* cover.

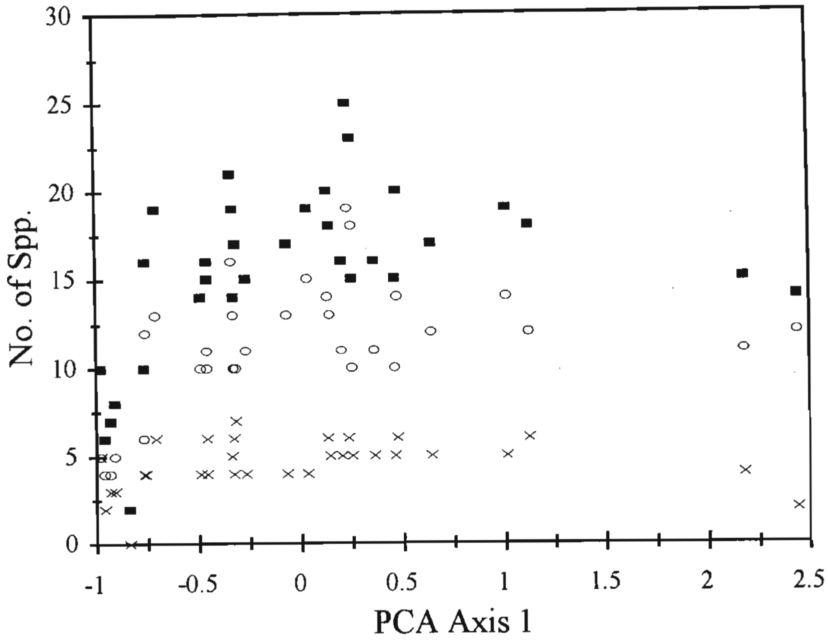


Figure 3.9 The relationship between the first PCA axis of the combined dune data and the number of annual species (open circles), perennial species (crosses) and the total number of species (squares).

Although historical and current grazing pressure were accounted for in the second PCA axis, the combined effect of all disturbance factors, the disturbance coefficient, was significantly correlated with the first PCA axis (Table 3.1). The condition score, based on functional groups, correlated positively with the first PCA axis (Table 3.1). The first PCA axis can thus safely be regarded as degradation gradient ranging from poor condition dunes on the left to good condition dunes on the right (Table 3.1). This is confirmed by the fact that the first PCA axis was very well correlated with litter cover, total herbaceous cover (Figure 3.5) and most of the important species as well as total nitrogen, phosphorus and organic matter. These relationships suggest that nutrients were lost where plant cover was reduced on the dunes (Table 3.2).

Although the most common species were linearly distributed along the degradation gradient (the first PCA axis) some of the less common species had a unimodal distribution (i.e. *E.*

lehmanniana & the cucurbits *Acanthosicyos naudinianus* and *Citrullus lanatus*) (Figure 3.6e&f). Only one species, *Hermannia tormentosa,* (perennial herb), occurred almost exclusively in degraded areas (Figure 3.6g), while a few, notably *Limeum arenicoloum,* (annual herb) (Figure 3.6h) occurred throughout the gradient. None-the-less, this did not negate the use of PCA because most of the species (which made up the largest proportion of the total cover) had a linear response along the first axis. There was no relationship between the woody cover (total or individual species) and the first ordination axis.

Only the smaller soil particles (<106 μm) were significantly related with the first PCA axis (Table 3.1, Figure 3.7). The second PCA axis is significantly correlated with the *B. glomerata* (palatable annual grass) cover, pH, total nitrogen and available phosphorus (Figure 3.8). Sites which, at the time of the study, experienced high grazing pressure were associated with the second axis (Figure 3.4). The relatively high cover of the annual grass, *B. glomerata,* may suggest that these sites are undergoing change from a dune dominated by perennial grasses and *S. kalahariensis* to one with low vegetation cover. Furthermore, the relatively high nutrient concentrations measured here suggest that the soil chemistry has not yet been altered as a result of the high grazing pressure.

The total number of species increased along the first PCA axis, but reached an asymptote near the origin (r=0.66 p=0.0004, log(X1+150)) (Figure 3.9). The number of herbaceous species per sampling area increased significantly with aerial plant cover, plant height, total nitrogen, available phosphorus and organic matter, but was negatively correlated with the disturbance coefficient (Table 3.2).

Table 3.1. The relationships between the causes and effects of degradation and the first and second PCA axis of the combined dune data.

Environmental variable	Axis 1	Axis 2
Causes of degradation		
Historical grazing pressure	-0.02 ns	-0.39*
Current grazing pressure	-0.00 ns	0.61***
Disturbance coefficient	-0.35*	0.04 ns
Fire	-0.5 ns	-0.37 ns
Condition score	0.88***	0.34 ns
Species aerial cover		
Schmidtia kalahariensis	0.99***	0.01 ns
Stipagrostis amabilis	0.69***	-0.06 ns
Centropodia glauca	0.46**	-0.00 ns
Brachiaria glomerata	0.07 ns	0.99***
Soil nutrients and vegetation cover		
Total phosphorus	0.72***	0.08 ns
Available phosphorus	0.27 ns	0.57***
Total nitrogen	0.46**	0.51**
Organic matter	0.57***	0.09 ns
pH	-0.34 ns	0.53**
Litter	0.82***	0.12 ns
Total Cover	0.82***	0.37*
Soil particle size classes		
425-500μm	-0.30 ns	0.24 ns
250-300μm	-0.08 ns	-0.18 ns
75-106μm	0.38*	-0.00 ns
53-75μm	0.43*	-0.10 ns

*: $p<0.05$; **: $p<0.01$; ***: $p<0.001$

Dunes versus interdunes

To test whether there was a relationship or interaction between the condition of dunes and the associated interdunes, correlations were done using variables from the dunes and interdunes respectively. There were no significant relationships between the respective PCA axis scores of the dune and interdune data. The only significant relationships were between the herbaceous cover on the dunes and the pH values recorded in the interdune ($r=0.46$ $p<0.01$) and between

Table 3.2 Correlations between important variables and the number of herbaceous species recorded on the dunes

Variable	Number of species
Disturbance coefficient	-0.661****
Total Cover	0.557***
Plant height	0.642***
Total nitrogen	0.764***
Available phosphorous	0.653***
Organic matter	0.462**

*: $p<0.05$; **: $p<0.01$; ***: $p<0.001$

herbaceous cover on the dunes and some of the soil particles sizes in the interdune, viz. the classes 500 to 1000 µm ($r=-0.37$, $p<0.05$); 53 - 75 µm ($r=-0.39$, $p<0.05$) and 75-106 µm ($r=-0.37$, $p<0.05$).

Dune aspects

Eigen values for the four PCA axes were 0.632, 0.188, 0.121 and 0.019. The first axis of the PCA plot was dominated by *S. kalahariensis*, while the second axis was determined largely by *S. amabilis*. *Stipagrostis amabilis* occurred almost exclusively on the dune crests and upper slopes, and therefore the crests were associated with the second PCA axis (Figure 3.10b). The slopes were distributed along the first PCA axis in relation to their cover of *S. kalahariensis*, whilst their distribution along the second axis was determined by their cover of *S. amabilis* (Figure 3.10b).

There were significant ($p<0.05$) relationships, similar to those described earlier for the combined dune data, between the two PCA axes and the cover of important species, nutrients and soil particles. Variables with more significance to the dunes crests, such as *S. amabilis* cover, were best correlated with the second axis, while those with more significance to the slopes, such as *C. glauca,* were better correlated with the first PCA axis. Consequently, all the degraded sites (irrespective of aspect) were situated near the bottom left hand corner of the ordination and dune crests improved in condition along the second axis while the slopes improved along the first axis.

Although the total herbaceous cover of the slopes and crest increased along the first PCA axis, the line depicting the herbaceous cover of the dune crests were consistently below that of the slopes (Figure 3.11), indicating lower plant cover on the dune crests along the entire gradient investigated. The Euclidean distance (Ludwig and Reynolds 1988) between the two slopes increased significantly along the first PCA axis ($r=0.45$ $p=0.009$) (Figure 3.12), indicating greater species differences between the two slopes at the good condition end of the gradient.

Sand Grain size distribution and nutrient levels of good condition sites

In order to illustrate the 'natural situation' regarding the grain size and nutrient distribution, the seven sites representing good condition rangeland furthermost to the right of the first PCA axis were analysed in relation to the distribution of these factors in the four sub-habitats studied.

Sand particle size composition differed according to position on the dune-interdune complex (Figure 3.13a,b,c). The interdunes had a higher proportion of small grains (e.g. 53 - 75 µm), but also contained more of the larger grains (500 - 1000 µm) than the dunes. Intermediate grain sizes were poorly represented in the interdunes by comparison with the dunes. Contrary to Lancaster's (1986) finding, dune crests had the highest proportion of intermediate particles and less large and small particles than slopes and interdunes.

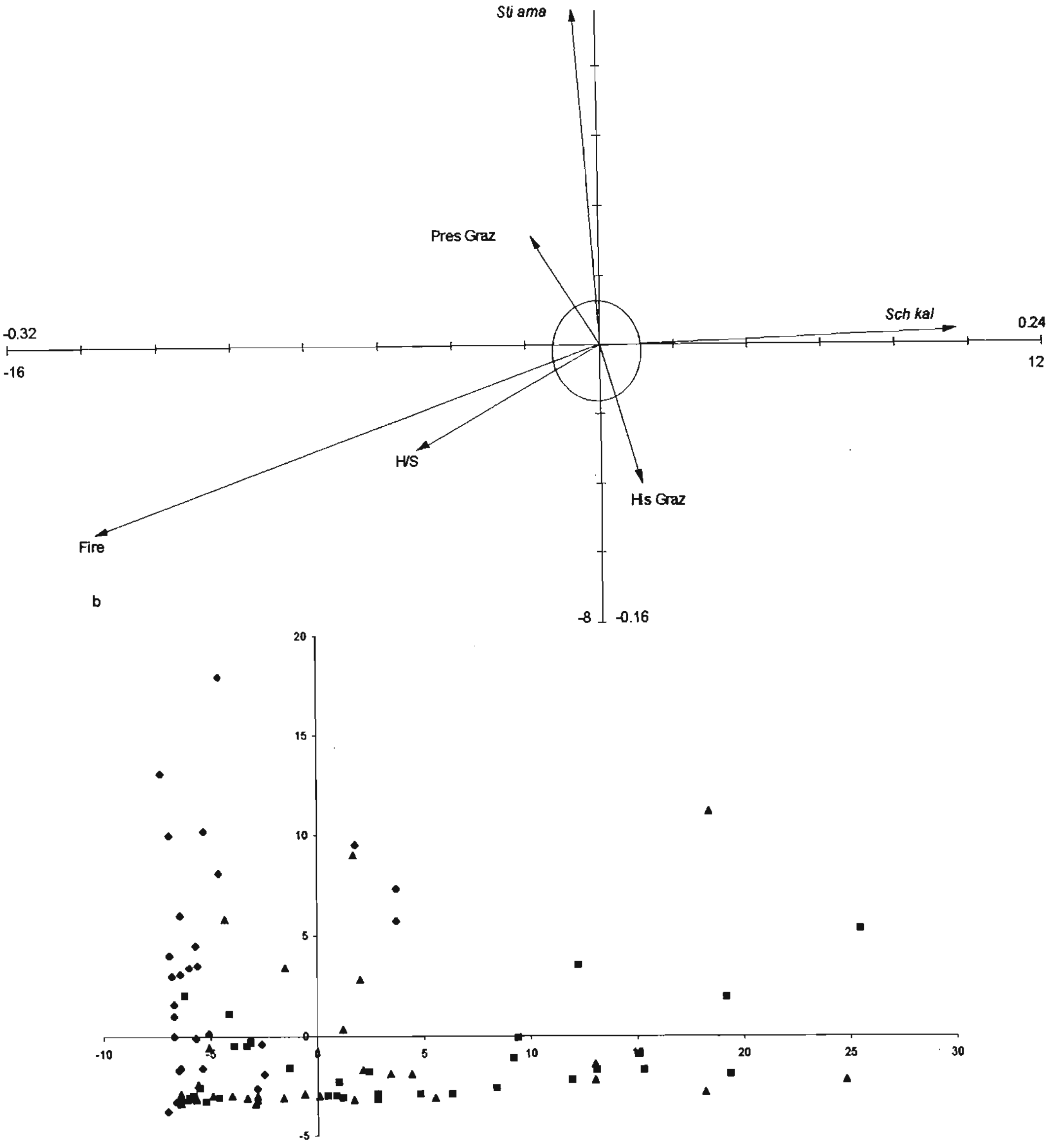


Figure 3.10 (a) A plot of species and environmental variables (arrows) and (b) sites (i.e. crests, ◆; SW slope, ▲; NE -slope, ■) in relation to the first two axis of the PCA. The ellipse on the origin of the species plot encapsulates several other species. The scale above the first and to the right of the second axis applies to the environmental variables. Pres Graz, His Graz, H/S and Fire refer the environmental variables: present grazing pressure, historical grazing pressure, proximity to homesteads and fire. Key to the grass species: *Sti ama, Stipagrostis amabilis*; Sch kal, *Schmidtia kalahariensis*; the other species *Brachiaria glomerata, Centropodia glauca, Eragrostis lehmanniana, Stipagrostis uniplumis, Hermanniana tomentosa, Senicio burchellii, Indigofera daleoides, Limeum arenicolum, Limeum fenestratum, Hermbstaedtia glauca, Melolobium macrocalyx, Acanthosicyos naudinianus, Citrullus lanatus, Gisekia africana, Stipagrostis ciliata, Crotolaria spartoides, Sesamum triphyllum, Tribulus zeyheri, Oxygonum delagoense, Crotalaria africana, Protasparagus nelsii, Limeum* spp, *Hermannia* spp, *Aptosimum procumbens, Aristida meridionalis.*

There were no differences in the distribution of available phosphorus across the sub-habitats, whilst total phosphorus concentration was significantly different only between the dune crest and interdune (Figure 3.14a,b). Total nitrogen and organic matter concentrations were significantly greater in the interdune areas than on the dune crests, while intermediate values were recorded on the slopes (Figure 3.14c,d).

There was a positive relationship between the proportion of small particles and the nutrient concentration in the soil samples analysed (Figure 3.15). Organic matter, total and available phosphorous and total nitrogen increased linearly with the proportion of small (53 - 75 μm) particles in a sample.

Sand movement

From the time series of standard deviations plotted in Figures 3.16a-c it is clear that there was no distinct seasonal variation in vertical sand movement. Although degraded dunes showed the highest variability, good condition dune crests and NE slopes did, however, experience short periods of activity. A two-way ANOVA of this data (Figure 3.17) indicated significant variation due to condition ($F=99$; $p<0.0001$) and aspect ($F=10.4$; $p<0.0001$) and a significant interaction between these two factors ($F=18.1$; $p<0.0001$). One-way ANOVA's on a reduced model indicated no differences between sand movement on the slopes and crests on good and intermediate condition dunes, while the south-western slope of degraded dunes experienced greater sand movement than the north-eastern slopes and crests. There was a significant ($r=-0.57$, $F=10.6$; $p<0.005$) negative relationship between aerial vegetation cover and the standard deviation of the sand movement (Figure 3.18).

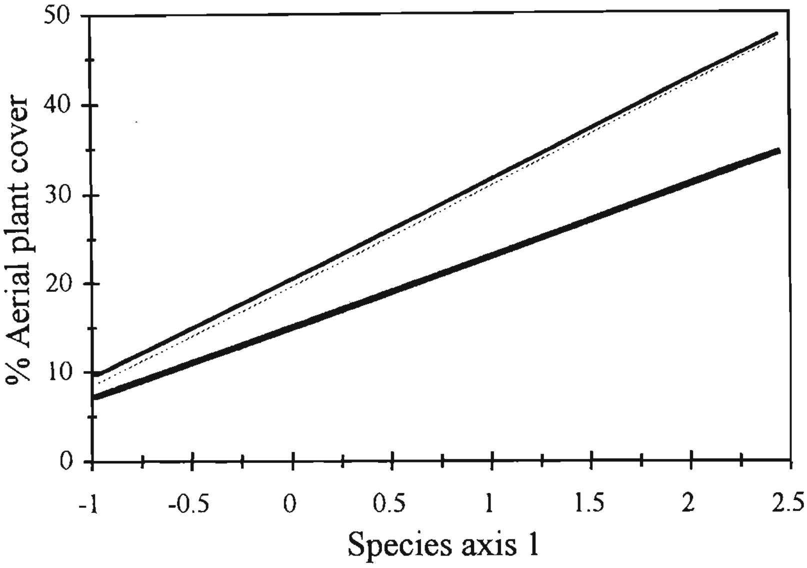


Figure 3.11 The relationship between the aerial plant cover of the crest (thick solid line, $r = 0.70$, $p < 0.0001$), NE slope (solid line, $r = 0.78$, $p < 0.0001$) and SW slope (dotted line, $r = 0.68$, $p < 0.0001$) and the first PCA axis based of the combined dune data.

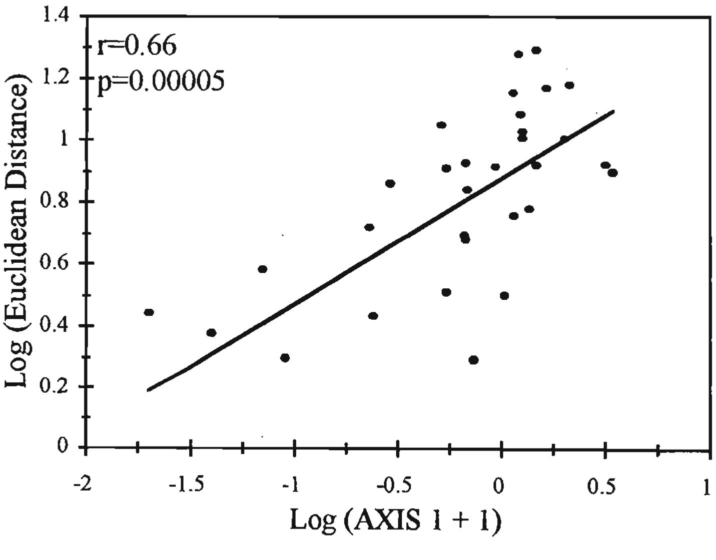


Figure 3.12 The Euclidian distance between the two slopes of each of the 32 sites in relation to the first PCA axis of the combined dune sites.

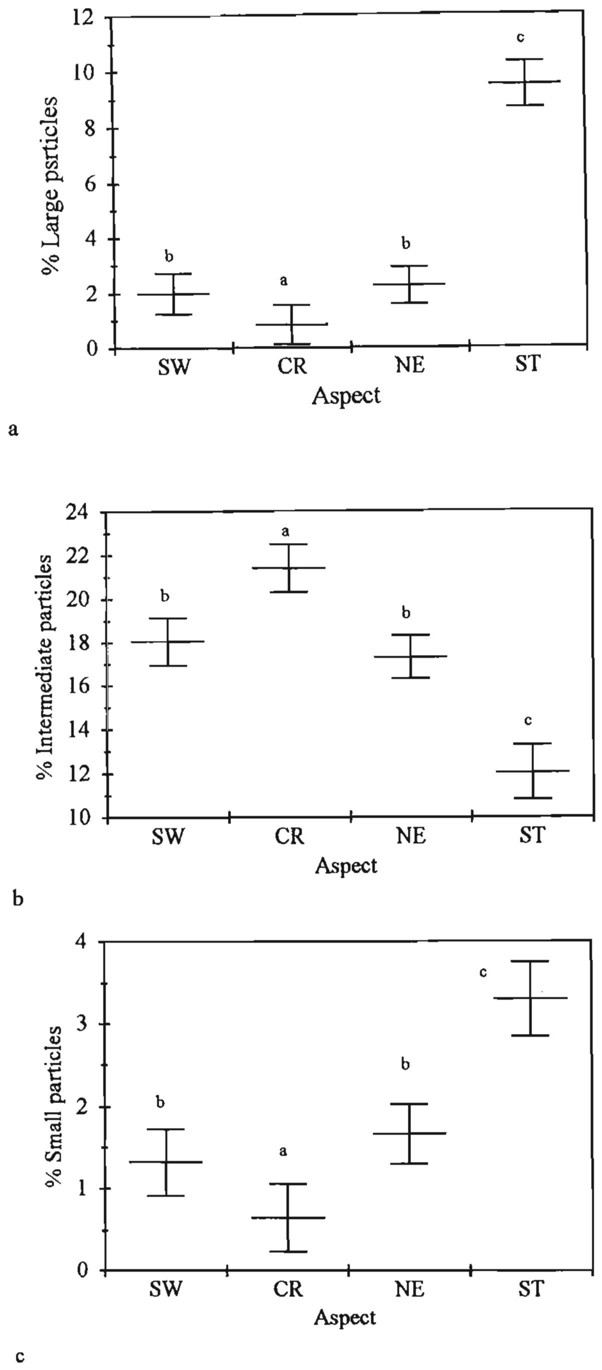


Figure 3.13 The distribution of large ((a) 500 - 1000µm), intermediate ((b) 212 - 250µm) and small ((c) 53 - 75µm) particle sizes of soil samples collected on the seven sites, furthermost to the right of the degradation gradient shown in Figure 3.4. The bars indicate the 95% confidence limits. Significant differences, based on 95% confidence intervals (one way ANOVA), between aspects are indicated with different letters. (SW: southwestern slope; CR: dune crest; NE: northeastern slope; ST: interdune).

Sand movement and small grain sizes were significantly negatively correlated (53-75μm $r=-0.79$; $F=9.3$, $p<0.05$ and 75-106μm $r=-0.76$; $F=11.8$, $p<0.05$). Small particles were thus eroded where sand movement was high, and were most probably deposited onto stable areas, where vegetation cover was high.

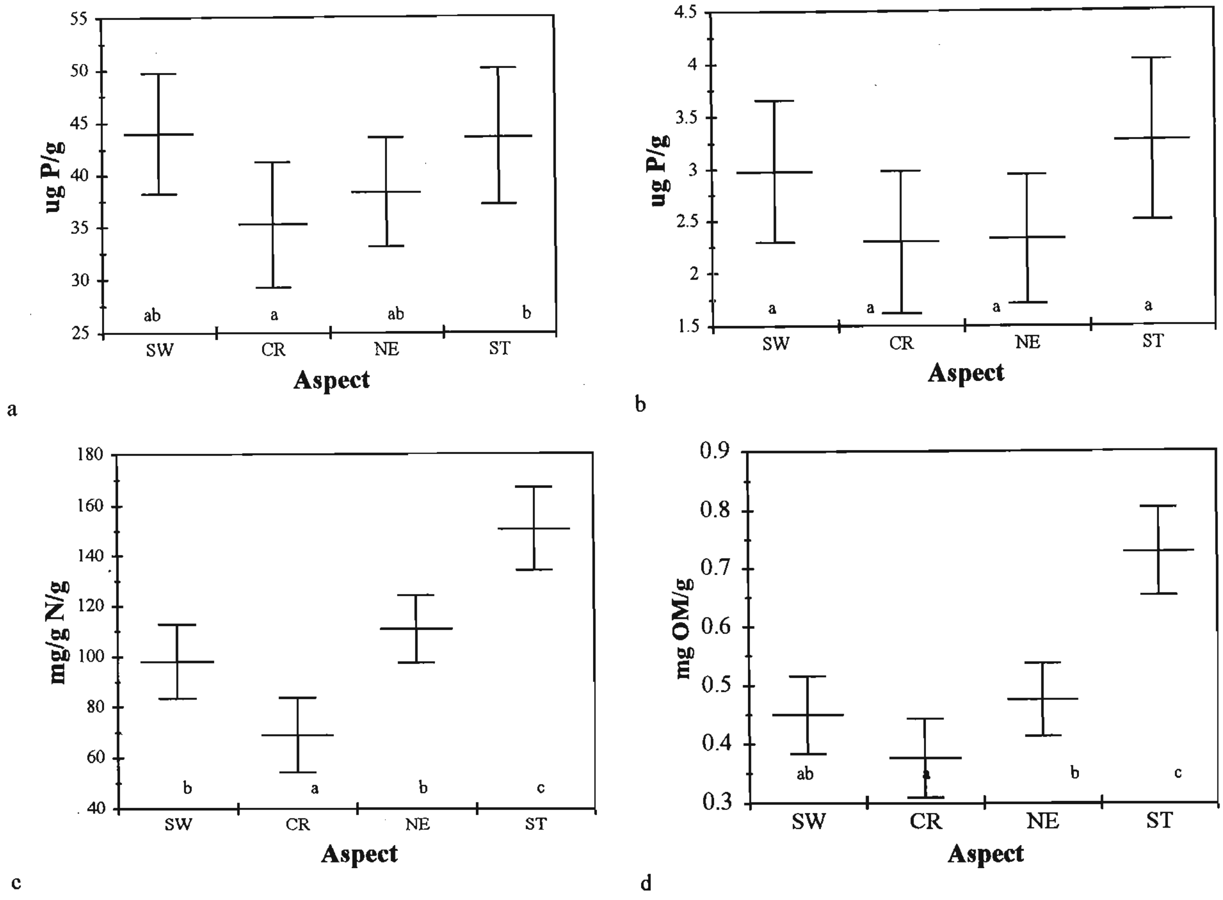


Figure 3.14 The distribution of (a) total phosphorus, (b) available phosphorus, (c) total nitrogen and (d) organic matter in soil samples collected on the seven sites, furthermost to the right of the degradation gradient shown in Figure 3.4. The bars indicate the 95% confidence intervals, significant differences, based on 95% confidence intervals (ANOVA), between aspects are indicated with different letters. (SW: southwestern slope; CR: dune crest; NE: northeastern slope; ST: interdune).

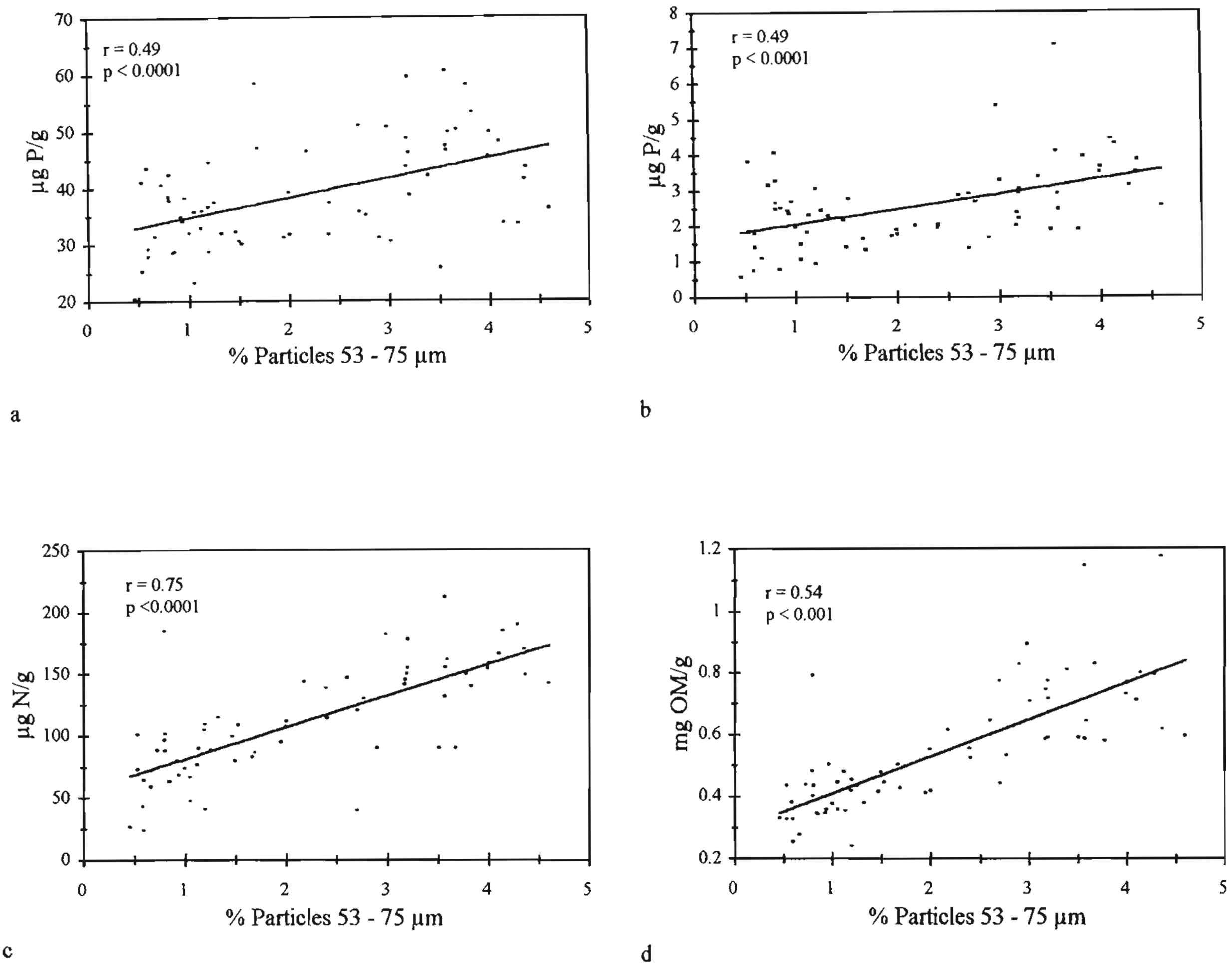


Figure 3.15 The relationship between (a) total phosphorous, (b) available phosphorus, (c) total nitrogen and (d) organic matter and the proportion of small particles in a soil sample.

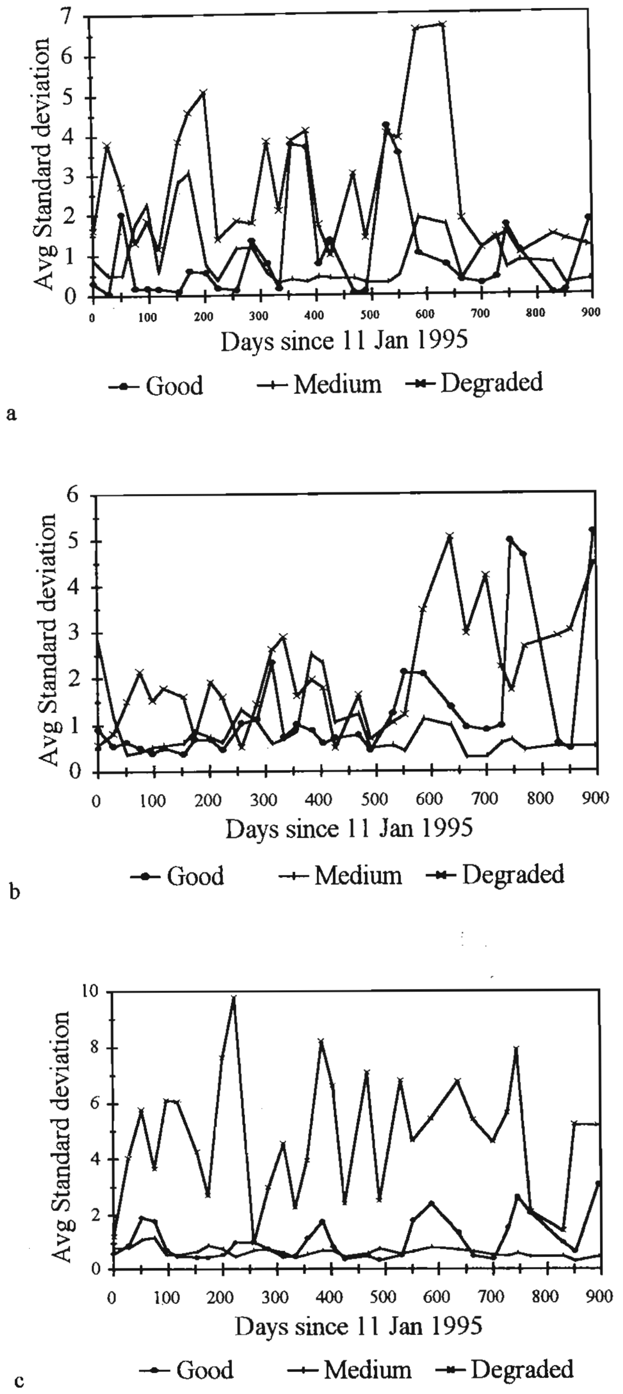


Figure 3.16 The vertical sand movement on the (a) NE slopes, (b) crests and (c) SW slopes on dunes in areas of good, intermediate and poor condition.

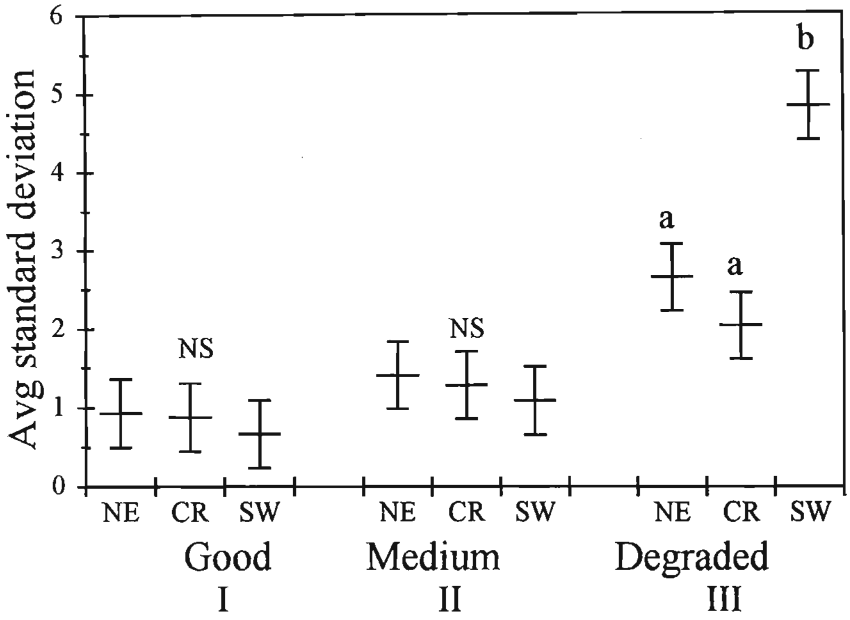


Figure 3.17 The average standard deviation of vertical sand movement on the dunes in areas of good, intermediate and poor condition. Different Roman numerals indicate significant differences between the relative condition classes, based on 95% confidence intervals of an ANOVA, while letters indicate significant differences between aspects within a condition class.

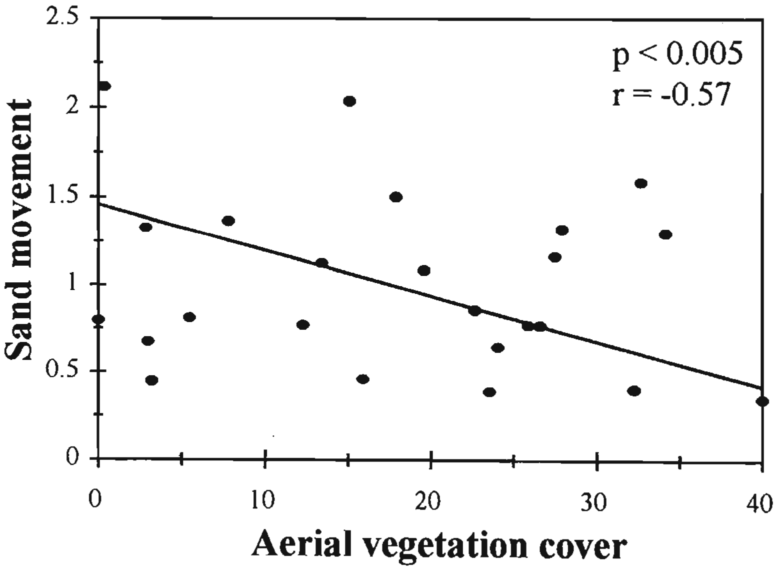


Figure 3.18 The relationship between aerial plant cover and the standard deviation of sand movement.

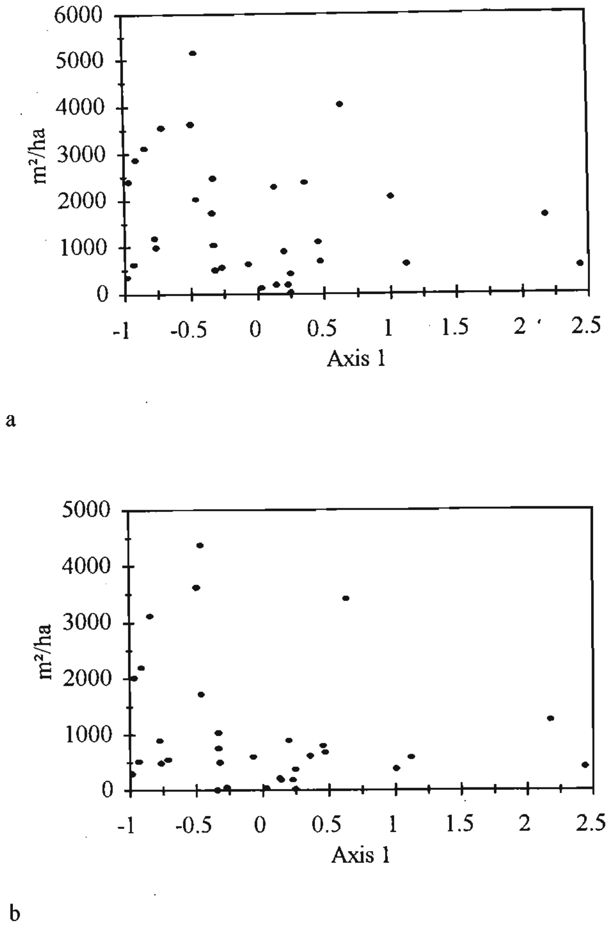


Figure 3.19 (a) The total woody cover on the dunes in relation to the first PCA axis. (b) The *A. haematoxylon* cover on the dunes in relation to the first PCA axis.

Woody vegetation cover

There was no statistically significant relationship between the frist PCA axis of the ordination and the cover or number of woody species. It is however important to note that, although some degraded areas may not have high cover of woody species, it is only degraded areas that have high woody cover. Good condition dunes always have low or no woody species cover.

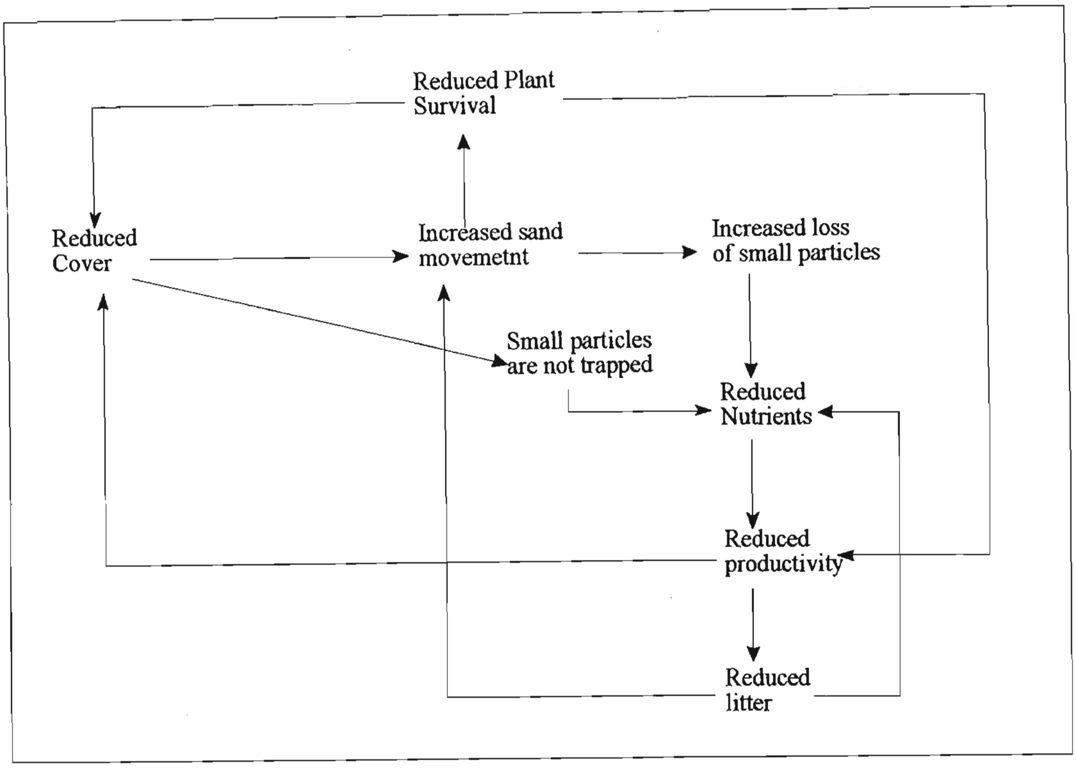


Figure 3.20 A hypothesised flow diagram of the processes which may result in stable degraded states in southern Kalahari rangeland.

Discussion

Vegetation

A distinctive characteristic of linear dune systems such as those in the southern Kalahari is the consistent repetition of landscape features. Dunes, which consist of slopes and crests, are interspaced by interdune areas. The different slopes of a dune facing in opposite directions potentially add another dimension to the landscape. These different 'habitat types' (south western slope, crest, north eastern slope and interdune, in the case of the southern Kalahari) provide different environments for plants, and may therefore react differently to disturbance. A prerequisite for describing the process of degradation in the southern Kalahari is a knowledge of the natural differences in the undegraded conditions and the manner in which sub-habitats differ.

Dunes and interdunes supported clearly distinct vegetation communities (Figure 3.2b). Wind velocity in the interdunes was slower (Figure 3.1) than on the dune crests, and therefore provided a more stable habitat in comparison with the high sand mobility of the dunes (Figure 3.16). Furthermore, nutrient concentrations (Figure 3.14) and soil particle size distributions (Figure 3.13) (that may influence moisture availability) differed between the dunes and interdunes. Although a few species occurred both on the dunes and in the interdunes, there were substantial environmental differences between these two habitats that would account for the distinct differences in species composition.

Interdunes on the left of the first PCA axis were associated with *C. glauca, B. glomerata* and *E. lehmanniana* (Figure 3.3a). Along the degradation gradient interdunes become increasingly dominated by *S. kalahariensis* (Figure 3.3a) and the shrub *R. trichotomum* (Moore 1989). There was no relationship between the condition (first PCA axis) of the dune and its associated interdune, indicating that these two areas react differently to disturbance. The only significant correlations found were (i) a positive relationship between the herbaceous cover of the dune and the pH of the soil in the interdune, (ii) a negative relationship between the herbaceous cover on the dune and the very small and very large soil particles in the interdune. These particles are probably lost from the dune and deposited in the interdune once vegetation cover is reduced (see section on Grain size distribution). Apart from this, which is purely a consequence of bare dunes losing certain grain sizes, there was no relationship between the condition of dunes and interdunes.

The interdunes seem to be more vulnerable to degradation than the dunes. Interdunes, with very low species diversity (*S. kalahariensis* and *R. trichotomum* dominant) are often seen in areas where the dunes are still well covered with perennial grasses (pers. obs.) The interdunes may be preferred grazing areas of mammalian herbivores because they are stable with low relief compared with the unstable steep slopes of the dunes. Furthermore, soil nutrient concentrations are higher in the interdunes resulting in vegetation with higher nutritional qualities than those growing on the dunes (AJ Stone unpubl. data). Finally, the lower moisture content of the interdunes (Chapter 4) (because of the shallow, compact soils, with different soil particle size distributions) may also contribute to its susceptibility to grazing impact.

The perennial grasses *S. amabilis* and *C. glauca* and the annual *S. kalahariensis* occurred in high densities on good condition dunes (Figure 3.2a). Good condition dune crests consisted mainly of the perennial rhizomatous grass *S. amabilis* with the annual grass *B. glomerata* present, but with much less cover (Figure 3.10a). The cover of these species decreased markedly (in a linear fashion) along the degradation gradient, resulting in dunes which are almost completely bare. Various forbs may occur on the dunes, but play a lesser role in the overall dynamics of the dunes. Two important dicotyledons, *Citrullus lanatus* and *A. naudinianus*, and the perennial grass *E. lehmanniana* seem to occur in higher densities on intermediate condition dunes (Figure 3.6e&f). This increase may be the result of increased moisture availability at lower plant cover, but due to high palatability (*C. lanatus* and *A. naudinianus* are very important sources of water for a host of mammals) these plants disappear completely in areas that experience high levels of grazing. On the other hand the toxic perennial herb, *H. tomentosa* (Leistner 1967) occurred almost exclusively on degraded dunes, while *L. arenicolum*, an annual forb with no grazing value, occurred throughout the degradation gradient (Figure 3.6g&h).

Very small soil particles are lost from the dunes as the vegetation cover on the dune is reduced, as shown by the proportion of small particles decreasing on the dunes during degradation (Table 3.1, Figure 3.7a). There is a negative correlation between the plant cover on the dune and the proportion of small particles in the interdune (Figure 3.18). Together with the small particles, organic matter is lost and this has the net result that nutrients are lost from the dune (Figure 3.5a,b,c) and are most probably deposited in the interdune areas. In addition to this loss of nutrients, less plant litter occurs on degraded dunes (Figure 3.5e) because plant cover is lower on degraded dunes (Figure 3.5f). This ultimately results in less nutrients released through decaying plant material and lower OM.

Woody species

The time frame in which woody plants react to disturbance is intuitively longer than herbaceous plants, and therefore woody plants were not included in the PCA. Woody plants on the dune crests are very scarce in good condition rangeland, while *A. haematoxylon*, *B. albitrunca* and *Lycium spp.* occur in low densities on the slopes. Degraded dunes had woody plant densities ranging from very low to high. The woody plant density in degraded areas may depend on the immediate local environmental conditions (i.e. factors controlling establishment and survival, including seed availability) and a time factor (woody plants on newly denuded dunes may still be in the process of establishing). *Acacia haematoxylon* establishes and grows successfully on degraded dunes and constitutes a large proportion of the woody species on degraded dunes (Figure 3.19b). The success of the woody species on the denuded dunes is most probably directly related to moisture availability. There is a negative (linear) relationship between herbaceous plant cover and soil moisture content (chapter 4). Soil moisture content on degraded dunes is high throughout the dry season allowing the plants to initiate growth once temperatures rise after the winter. This process of woody invasion (or increasing woody density) most probably follows the same mechanism as described by Skarpe (1990a, 1990b).

The same phenomenon occurs in the interdune areas, where *R. trichotomum* increases dramatically during degradation (Moore 1989). *Rhigozum trichotomum* normally occurs locally in small groups in the interdunes especially in shallow areas such as those around pans (Leistner 1967). These plants increase to very high densities where the grass layer is removed, and are capable of surpressing the grass layer once established (Moore 1989).

Plant diversity

There was a positive relationship between the total number of plant species present on the dunes and rangeland condition, plant cover, OM, total P and total nitrogen (Figure 3.9, Table 3.1). Although there was a marked increase in the number of species between the degraded end of the first PCA axis and the origin (Figure 3.9), thereafter it seemed to reach an asymptote (if not a decline). Plant diversity is thus only severely reduced towards the degraded end of the scale. The functionality of the dune system, however, is severely compromised with the reduction (not only complete loss) in the cover of one species, *S. amabilis*. *Stipagrostis amabilis* occurs almost exclusively on dune crests and is the only species capable of stabilising dune crests. Once its cover is markedly reduced, excessive sand movement prevents the establishment of seedlings and erodes existing vegetation. This species may thus be regarded as a driver species (Walker

1992) as even its partial removal has significant impacts on ecosystem functioning (see O'Connor 1995). Various other species are important from an animal production point of view, but their loss does not impair the systems functionality as such. Reduced cover of species such as *C. glauca* may expose *S. amabilis* to higher wind speeds around the root zone which may eventually lead to their demise through erosion, but this 'protective role' may, however, be played by other species such as *Eragrostis lehmanniana* or *S. uniplumis*.

Grain size distribution and soil nutrient concentrations

The grain size distribution along the dune/interdune profile is of importance, not only because it influences the moisture availability (through capillary forces) but also nutrient availability. Lancaster (1986) described two main grain size and sorting patterns in desert sand dunes. In the first model, dune crests and slip faces are finer, better sorted and less positively skewed than the dunes flanks and interdune areas. In the second model, first described by Folk (1971), the dune crests are coarser, but better sorted than flanks and interdunes areas. Lancaster (1986) found most of his sites, which included areas within this study area, accorded with the second model, apart from four sites where interdune sediments contained a high proportion of coarse grains. In the present study, interdune areas contained much more coarse (and fine) particles than the dunes and the dunes and slopes consisted of largely medium size particles (Figure 3.13). Other grain characteristics (e.g. skewness and kurtosis) were not studied. Although Lancaster (*op cit.*) did report differences in grain characteristics between flanks and dune crests at the regional scale, he did not investigate the effect of vegetation cover.

In this study, grain size distribution was influenced by both sub-habitat (Figure 3.13) and rangeland condition (Table 3.1, Figure 3.7). In a linear dune system in Israel, Kadmon & Leschner (1995) also found the dune crest to contain the lowest proportion of fine particles. The most prominent changes were a decrease in the smaller grain fraction on the dunes along the degradation gradient (Figure 3.7a). This is in accordance with Sterk *et al.* (1997) who found that the larger particles are transported by saltation, over short distances, while small particles are transported higher above ground level, and transport of these particles is subsequently further.

Buckley and co-workers (Buckley 1981, Buckley *et al.* 1987a, 1987b), described the nutrient distribution of the southern Kalahari dunes and interdunes. They did not investigate the effect of rangeland condition on the nutrient distribution, but their results can be summarised as follows. There is a general increase in total soil nitrogen going from the dune crest to the interdune with the surface layers having consistently higher total nitrogen levels than the deeper layers (Buckley *et al.* 1987a). Phosphorus, Ca and K did not show the same distribution as nitrogen, but P and K were also consistently higher on the surface than deeper. Calcium concentrations were higher in the deeper layers. The present study did not investigate nutrient levels deeper in the soil profile but found similar habitat differences for nitrogen (Figure 3.14c). Available phosphorus in good condition dunes did not show any pattern down the dune interdune profile (Figure 3.14b) (see also Buckley *et al.* 1987b).

Organic matter, available P and total N are lost from the dunes during rangeland degradation (Figure 3.5) and so are the smaller soil particles (Figure 3.7). The nutrients are most probably deposited in the interdunes, but no increase in nutrients was observed during this study. There was, however, a negative relationship between the vegetation cover on the dune and the proportion of small particles in the interdune soil. Good vegetation cover thus prevents the loss of small soil particles and nutrients. The nutrients are most probably deposited in the interdunes, but the relatively large size of the interdunes compared with the dunes (class 2 dunes; Bullard *et al.* 1995) probably masks its effect, or these nutrients are captured by the plants growing in the interdunes.

Gupta et al. (1981) studied soil erosion and associated nutrient loss in the sandy soils and dunes of western Rajastan, India. Their results on the relationship between grain size and the nutrient content of a specific grain size fraction, indicated that the nutrient content (OM, P, N & K) of the smaller fractions were much higher than in the larger fractions. Although not specifically tested, similar trends are evident for the southern Kalahari. OM, N and P levels correlated well with the proportion of small grains in the samples studied (Figure 3.15), suggesting that the smaller fraction contains the highest nutrient levels. Sterk *et al.* (1997) also found that the finer (suspended) particles caught higher off the ground in sediment catchers contained significantly higher nutrient concentrations than the larger particles.

Gupta *et al.* (1981), however, found that the smallest particles are the least easily eroded, while particles ranging between 0.1 and 0.25 mm are the most easily eroded soil particle sizes. The small particles are trapped within the larger particles (Warren 1972) explaining why they are the least easily eroded. Furthermore, this is a possible explanation for the interdunes being associated with both large and very fine grains. With a loss of vegetation cover, and subsequent increase in sand movement, large particles are transported down the dune slope and because of its size may well be limited to a net movement down the slope. Intermediate particles as indicated by Gupta *et al.*(1981) may well be blown back onto the dune.

Fine grains are also lost from the dunes because the sand on degraded dune crests and flanks are continuously turned, exposing the fine grains, from where they are then deposited in the interdune areas. The smaller, suspended, particles carry the most nutrients over longer distances, and therefore probably increase the nutrient status of the interdunes, as it is suspected that at least a portion are deposited onto the interdune areas, because of lower wind speeds over these areas.

This phenomenon has two important implications for rangeland dynamics in the Kalahari. Valuable nutrients are lost from the dunes and flanks, which, together with increased sand movement, may prevent the recolonisation of degraded dunes. In addition, as the fine grains are not easily removed from the interdunes once they are embedded amongst the large particles and protected from erosion by the large particles (Gupta *et al.* 1981). Their redistribution against gravity to the crest is thus highly unlikely. These nutrients are therefore effectively lost from the dunes, a factor that may ultimately impair primary production and hinder the re-establishment of vegetation. Secondly, the increased nutrient levels in the interdune areas may have profound effects on the functioning of that system. Nutrients lost from the dunes may become incorporated in 'fertile islands' beneath *R. trichotomum* improving their nutrient budget, and adding to the heterogeneous distribution of soil resources in the interdunes. In disturbed areas where *R trichotomum* has not yet increased, or where they may have been chemically controlled, the annual grass *S. kalahariensis* may benefit from the increased nutrient levels, adding to their vigour and competitive ability. This may explain why interdune productivity is not impaired during rangeland degradation as found by Stone (unpubl.).

Sand movement and cover

The role of vegetation on the dynamics and structure of linear dunes has been recognised (Livingstone & Thomas 1993, Tsoar & Møller 1986, Thomas 1988, Thomas & Tsoar 1990) and was recently investigated in the southern Kalahari (Wiggs *et al.* 1994, 1995, 1996). Sand movement is generally higher on the dune crests than elsewhere (Kadmon & Leschner 1995). This is in reaction to the higher wind speeds experienced on dune crests (Figure 3.1) (Mason & Sykes 1979, Lancaster 1985). However, sand movement needs to be quantified in order to illustrate its role in changing the functioning of the degraded system. Sand movement and vegetation aerial cover is significantly negatively correlated (Figure 3.18). This study supports the studies of Wiggs *et al.* (1995) who found that a gradient of activity in relation to vegetation cover is evident rather than a threshold value beyond which the dune becomes active (Figure 3.18). Good condition dunes were found to be the least active (they have the highest cover, litter (Table 3.1) and height (Table 3.2) values, with no difference in activity between the slopes and crest. The crests and NE slopes sometimes experience short periods of high activity while the SW slopes of good and intermediate condition dunes are very stable, but experience very high activity levels once degraded (Figure 3.17). The NE slopes and crests of degraded dunes were not as active as the SW slopes (i.e. slip-face). Degraded dune crests were not as active as that would be expected with very little vegetation cover and litter and dunes crests experience higher wind velocity (Figure 3.1). This may be the result of a monitoring bias, as only vertical movement can be measured by the method employed. This method provides no information on the sand that passes through the measuring site where such movement of sand does not alter the level of sand in relation to the measuring rod. This is a common shortcoming of this technique

(Wiggs *et al.* 1995). The use of sediment traps, as used by Sterk *et al.* (1997), may provide more accurate information regarding horizontal sand movement while also providing clearer information concerning the redistribution of nutrients.

Conclusions

Vegetation cover is most probably the single most important factor determining the functioning of the dune system. The consequences of disturbances such as fire and heavy grazing, which reduce vegetation cover, may have lasting effects on ecosystem functioning. Loss of cover stimulates a series of positive feedback mechanisms (Figure 3.20) that prevent recovery of vegetation, even after the original disturbance has ceased. Reduced cover results in increased sand movement, which results in a loss of small soil particles. Nutrients are strongly associated with the small grain fraction and the nutrient status of the dunes is thereby reduced. Excessive sand movement also prevents the successful establishment of seedlings (by erosion, inundation, and physical damage) and hence the primary productivity on the dunes is reduced. The high nutrient levels in the interdune areas benefit *S. kalahariensis* and *R. trichotomum*, which do not contribute substantially to the diet of either domestic or indigenous herbivores. Once invaded by these two species, the interdunes can no longer support the grazing animals that are now forced onto the dunes. This further increases the grazing pressure on the dunes adding greater momentum to the positive feedback processes of degradation. Various other factors may also contribute positively to the maintenance and/or further degradation of the system (e.g. reduced seed banks chapter 7, soil micro-organisms (Allsop & van Rooyen unpubl.) and increased surface wind velocity (Wiggs *et al.* 1995)).

The stable degraded vegetation state described here is thus maintained by: (i) continued sand movement on the dunes because of a lack of vegetation on the dunes that can stabilise it to ensure (ii) seedling survival and (iii) the deposition of fine particles to rebuild nutrient and soil micro-organism concentrations and most importantly (iv) a source of perennial grass seeds because the greatly reduced perennial grass seed bank of degraded areas is under increased predatory pressure (Chapter 7). Degraded southern Kalahari rangeland is thus highly unlikely to recover within a time frame acceptable to the land user without intervention.

Chapter 4

Soil moisture dynamics in the southern Kalahari: The interaction between dune soil moisture and range land degradation

Introduction

Degraded dune fields in the southern Kalahari are characterised by bare mobile dunes, often with greater woody vegetation cover than undisturbed dunes (Chapter 3). Recovery from a degraded state is either very slow or does not take place at all. Changes in ecosystem functioning that may prevent natural recovery include changes in nutrient status, increased surface instability on the dunes (chapter 3) and changes in the seed bank and rates of seed predation (Chapter 7).

Water is generally regarded as the most important limiting factor for plant productivity in arid and semi-arid areas (Noy-Meir 1973; Snyman *et al.* 1987). Several authors have described the negative effect of increased grazing pressure on moisture dynamics through reduced infiltration and increased run-off (Kelly & Walker 1976; Snyman & Fouche 1991; Dean 1992). There is, however, often an increase in soil moisture content with reduced plant cover (Link *et al.* 1994; Waugh *et al.* 1994) for soils that readily absorb water. Most soils with higher clay content harden easily or become 'capped' during degradation with the result of reduced infiltration. Snyman and Fouche (1991) described reduced rain-use efficiency in medium and poor condition rangeland and ascribed the differences mainly to increased run off in poor condition rangeland. In the study referred to above, the interaction between water availability and other factors that reduce primary productivity (e.g. changes in species composition) becomes muddled. The sandy soils of the Kalahari, with the high filtration rate associated with sandy soils (Tsoar 1990), allow the study of the effects of degradation on plant dynamics without the confounding effects of increased run off and consequent reduced moisture status of degraded rangeland.

The key questions asked during this study were: (i) How does rangeland degradation (plant cover or biomass) influence the soil moisture status in the southern Kalahari? (ii) What are the consequences of this for (a) vegetation dynamics, and (b) management of degraded areas?

Methods

Automatic weather station

An automated weather station was set up during early January 1995 in the study area. Daily rainfall, humidity, wind speed and light intensity were recorded for the study period (January 1995 - July 1997). In addition, rain gauges were erected at each of the research sites that were monitored for soil moisture. Rainfall was recorded approximately once a month, at the same time soil moisture readings were made.

Soil moisture

Volumetric soil water content (Θ) was monitored on the dune crests of ten sites representative of good (n=3), degraded (n=4) and intermediate (n=3) condition range land, using a neutron probe (Model 503, Hydro probe, Campbell Pacific Nuclear, Pacheco, California). The relative rangeland condition classes were based on the cover of perennial grasses, and this classification was confirmed with the results of a PCA based on the vegetation cover of a range of sites in varying condition. Calibration of volumetric water content (gravimetrically determined) against neutron probe standard counts was done following Link *et al.* (1994). All measurements were taken at 10cm intervals to a depth of 120 cm in aluminum access tubes (5cm inside diameter). Soil bulk density was recorded at various levels, but bulk density remained constant at 1.756 g/cm down the entire profile. There was a highly significant correlation between neutron probe count ratios and gravimetrically determined soil moisture levels at all levels ($r = 0.76$; $p < 0.0001$). Neutron probe measurements close to the soil surface are generally not reported because of half sphere errors near the surface. However, there was also a significant correlation between neutron probe count ratios and gravimetrically determined soil moisture levels at 10 and 20 cm depths ($r=0.89$, $p<0.00001$).

Soil water storage (S), the integrated amount of water in the profile, expressed as a depth of water (mm), was determined following Green *et al.* (1986).

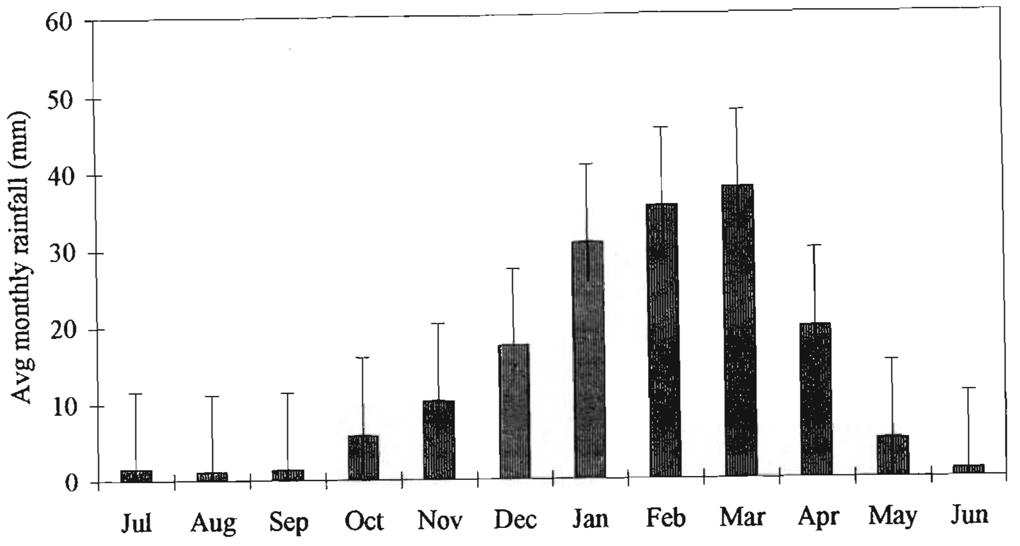
Vegetation

Plant species composition and litter cover were determined (Chapter 3) on each of the dunes where moisture was recorded at the end of the growth seasons of 1995 and 1996.

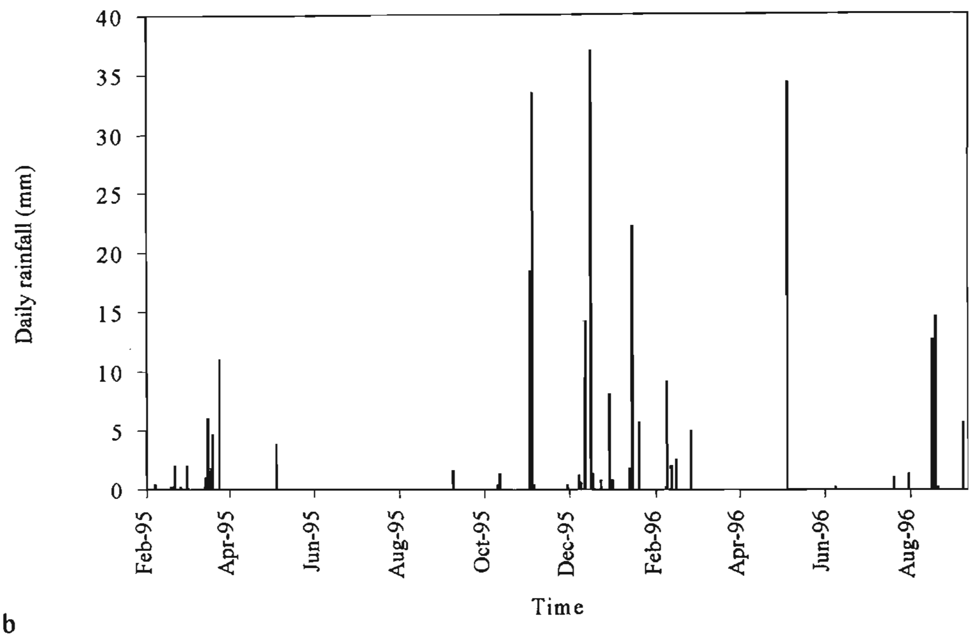
All statistical analysis was done using one- and two-way analysis of variance, regression and correlation analysis using Statgraphics IV (Statgraphics 1991).

Results

Daily rainfall is illustrated in Figure 4.1. Total rainfall from Jan 1995 to July 1995, when the first vegetation surveys were done, was markedly lower than for the six months preceding the 1996 vegetation surveys. Consequently, total soil water storage (S) was relatively low during the period Jan 1995 to October 1995 in all three condition classes (Figure 4.2 a-c). After the rain during December 1996, S increased and remained relatively high during the rest of the study period. However, to illustrate the interaction between wet and dry periods, rangeland condition and depth, an analysis of volumetric soil water content (ϴ) was done for the period Sept 1995 (after a relatively long dry period) and March 1996 (following a relatively wet period). Two separate two-way ANOVAs showed that ϴ was significantly affected by rangeland condition and depth for both wet (condition: F=129.9, depth: F=64.7 with, $p<0.0001$) and dry periods (condition: F=125.9, depth: F=25.1 with $p<0.0001$) (Figure 4.3). Degraded rangeland had higher ϴ values during both wet (t=10.26; df: 11; $p<0.001$) and dry (t=4.17; df: 11; $p<0.01$) conditions. Although there was no significant difference between medium and good condition rangeland, ϴ in good condition rangeland was consistently lower than in medium condition areas. A decomposed model indicated that there was no difference in ϴ close to the surface during dry periods, but deeper down the profile (> 40 cm) degraded areas were significantly wetter (F=7.7 with $p<0.0001$) (Figure 4.3a(iii)). The condition-by-depth interaction was not significant during the wet period (March 1996, Figure 4.3biii), but degraded areas were still moister than rangeland in medium or good condition. In addition, a two-way ANOVA of condition by time (wet / dry) revealed a significant interaction between condition and time (wet/dry periods) (F=9.23, $p<0.0001$). The increase in ϴ during the wet period was much greater for degraded rangeland than for rangeland in good or medium condition (Figure 4.3a and b).



a



b

Figure 4.1 (a) The average monthly rainfall at Rietfontein for the period 1912 - 1994, bars indicate 95% confidence limits (n=85). (b) The daily rainfall measured in the study area during the period 11 January 1995 to 30 November 1996.

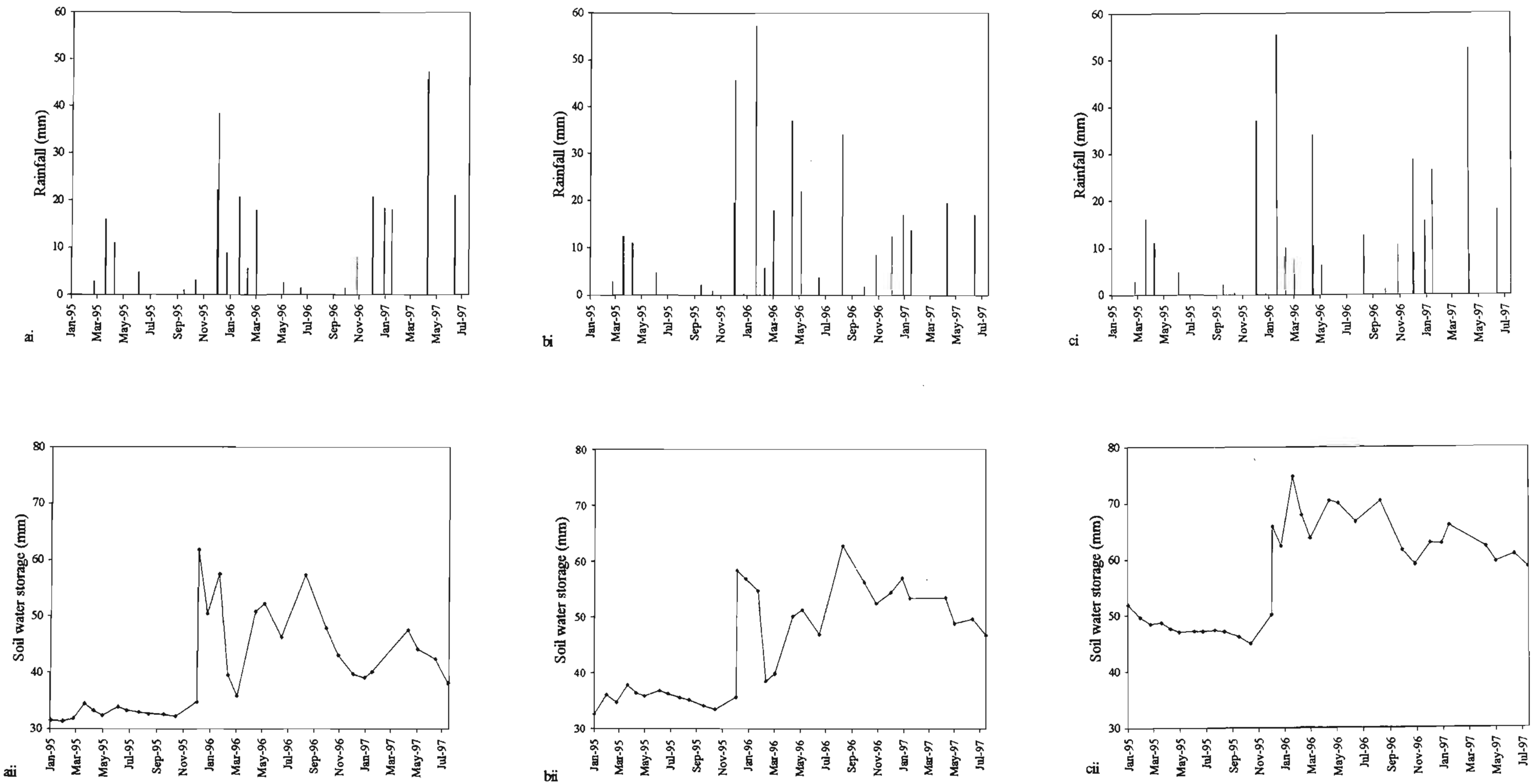


Figure 4.2 (i) The average monthly rainfall at each of the sites in (a) good, (b) medium and (c) degraded rangeland, as well as (ii) the total soil water storage (10 to 120 cm depth) at the same sites. N = 3 in all cases apart for sites in degraded rangeland where n = 4.

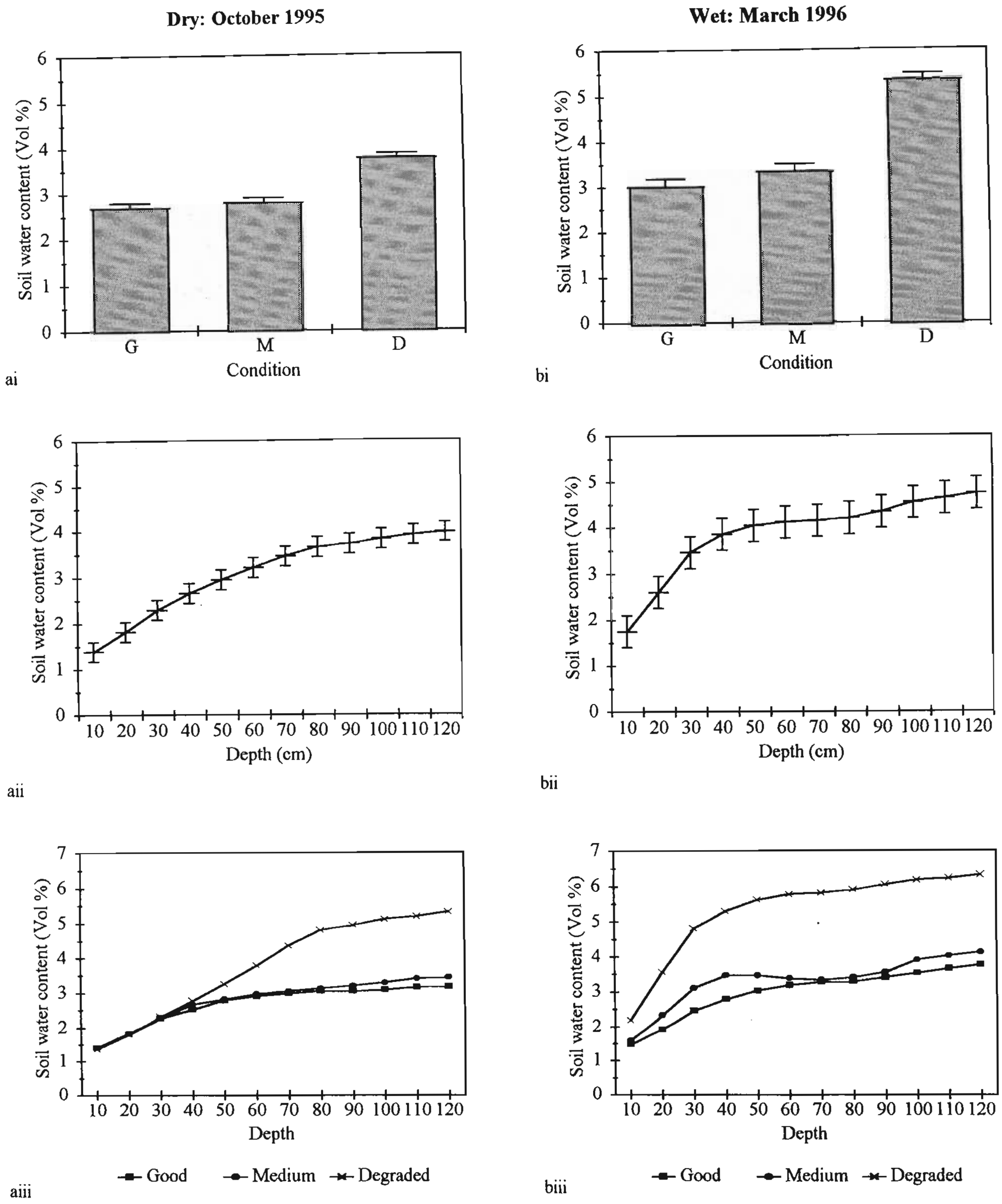


Figure 4.3 Total soil moisture at various depths in rangeland of different condition, during a (a) dry and (b) a wet period. Differences in soil moisture content is indicated in relation to (i) rangeland condition, (ii) depth and (iii) the interaction between depth and condition. Bars in all graphs are 95% confidence limits.

The relationship between ϴ and plant cover (an index of rangeland condition on dunes) was further illustrated by the negative correlations between ϴ and plant cover at different depths down the profile for both the 1995 and the 1996 vegetation surveys (Table 4.1). In addition, plant height was recorded at monthly intervals at the same time as moisture monitoring. This database was used to correlate soil moisture at the 12 depths with plant height. Soil moisture and plant height was weakly (but significantly) negatively correlated close to the soil surface, but the strength of the negative correlations increased down the profile (Figure 4.4). Larger negative r-values with depth, describe drier soil conditions deeper down the profile in areas with higher vegetation.

Table 4.1 Correlation coefficients between soil moisture content and plant cover at different depths during July 1995 and 1996

Depth	1995	1996
10	ns	ns
20	ns	ns
30	ns	ns
40	-0.82**	ns
50	-0.90***	ns
60	-0.84**	ns
70	-0.79*	ns
80	-0.77*	ns
90	-0.75*	ns
100	-0.69*	-0.67*
110	ns	-0.75*
120	ns	-0.77**

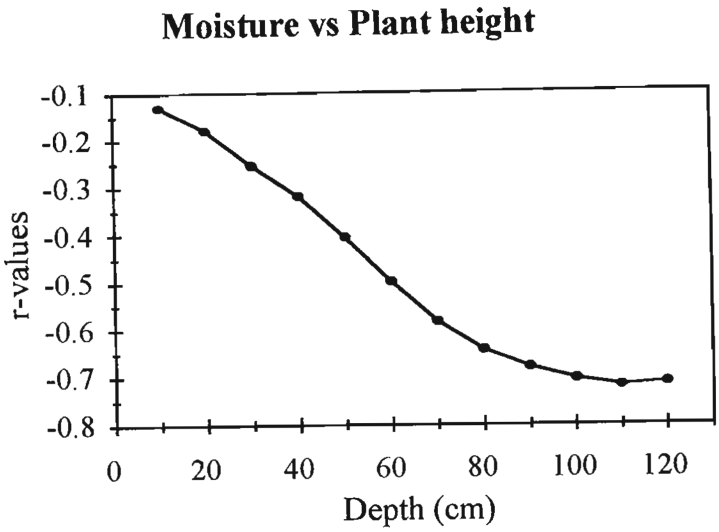


Figure 4.4 A plot of correlation coefficients between plant height and soil moisture at depths ranging from 10cm below the surface to 120cm below the surface. All the r-values were statistically significant.

Figure 4.5a-c illustrates changes in soil moisture after a relatively long period of limited rainfall, followed by two rainfall events. Moisture levels on 23 Oct 1995 were higher in degraded dunes ($F=129.9$, $p<0.0001$) than in good or medium condition dunes. The effect of a rainfall event (20mm) on 10 Dec produced changes in soil moisture up to 50 cm in depth recorded 24 hours later on the 11 of Dec 1995. Further rainfall (40mm) on the 12 of Dec resulted in recharge of at least the top 100cm. Differences between soil moisture levels at all levels between the condition classes at this stage (14 Dec) are trivial. However, by the 3rd of January 1996, soil moisture levels were once again different ($p<0.05$) between the condition classes. Moisture in the degraded areas remained relatively high, while it was rapidly depleted in areas of good condition. The differences between moisture levels of degraded areas and good areas, and between degraded and medium condition rangeland in relation to depth, are illustrated in Figure 4.6a&b. Some 20 days following the Dec 10 and 12 rainfall events, there was a small but consistent difference in moisture content between degraded and medium condition dunes. Good condition dunes were on the other hand clearly much drier. After a relatively long dry period, medium condition dunes approached the low soil moisture levels found in good condition dunes (Figure 4.6a).

Evapotranspiration

To determine differences in evapotranspiration between the condition states using the simplified equation as done by Link *et al.* (1994) proved unsuccessful. Small differences in rainfall between the sites resulted in unacceptable large differences in evapotranspiration. However, no rainfall occurred during the period 14 Dec 1995 to the third of January 1996, and as soil moisture was recorded on both dates at all sites, evapotranspiration and deep drainage was calculated merely as the difference in soil water storage. The loss in soil water storage during these 20 days after approximately 60 mm of rain were 0.578, 0.518 and 0.195 mm/day for good medium and degraded rangeland. Assuming that deep drainage is similar in the different condition classes, it is evident that evapotranspiration in good condition rangeland is higher than in medium and degraded rangeland.

Vegetation

Plant cover was different between condition classes in both years sampled. Total rainfall in the six months prior to the July 1995 and July 1996 vegetation sampling periods was 35 and 150 mm respectively. This resulted in significant increases in total ($F=91.1$, $p<0.0001$) and annual vegetation cover ($F=109.7$, $p<0.0001$), but there was no increase in perennial plant cover. Significant condition-by-year interactions indicated that rangeland in different condition responded differently to changes in rainfall (Figure 4.7) with regard to total ($F=13.1$, $p<0.001$) and annual plant cover ($F=11.2$, $p<0.01$).

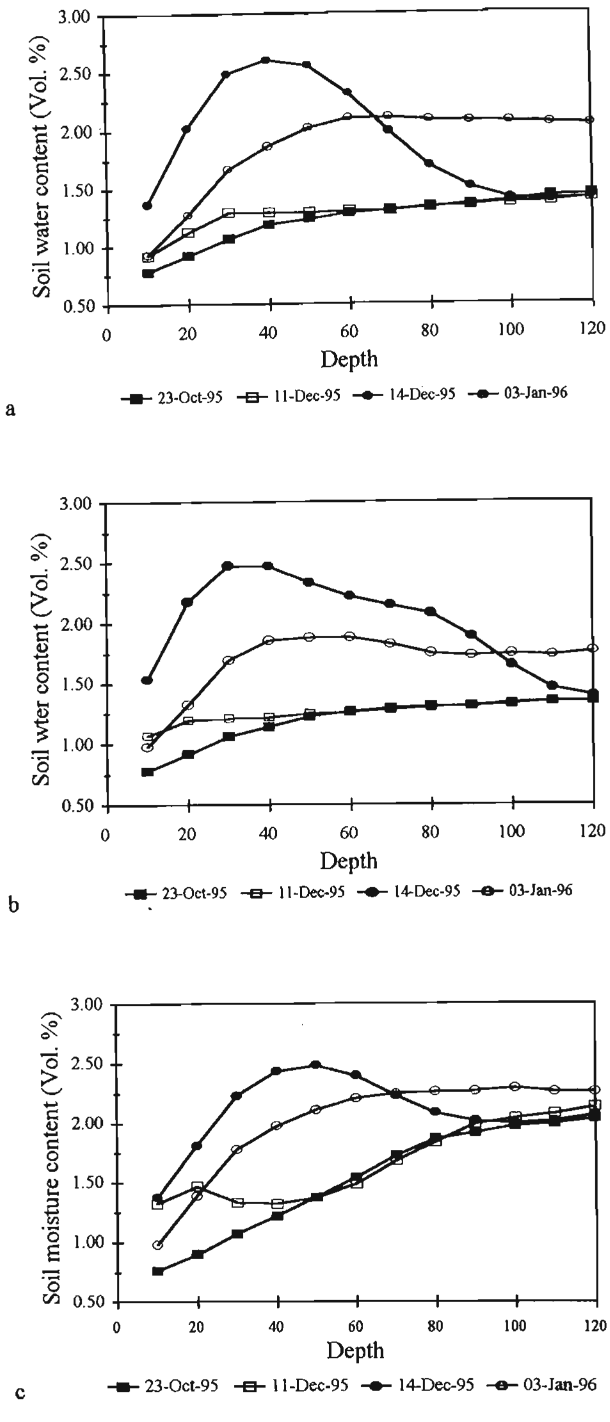


Figure 4.5 Soil moisture content between 10 and 120cm below the surface, measured on dune crests in (a) good, (b) intermediate and (c) degraded rangeland. Moisture by depth profiles were recorded on 23 Oct 1995 (at the end of a dry period), on 11 Dec 1995 (after 20 mm of rain on the 10 of Dec 1995), on 14 Dec 1995 (after a further 40 mm was recorded on the 12 of Dec 1995) and on the 3rd of Jan 1996. See text for details.

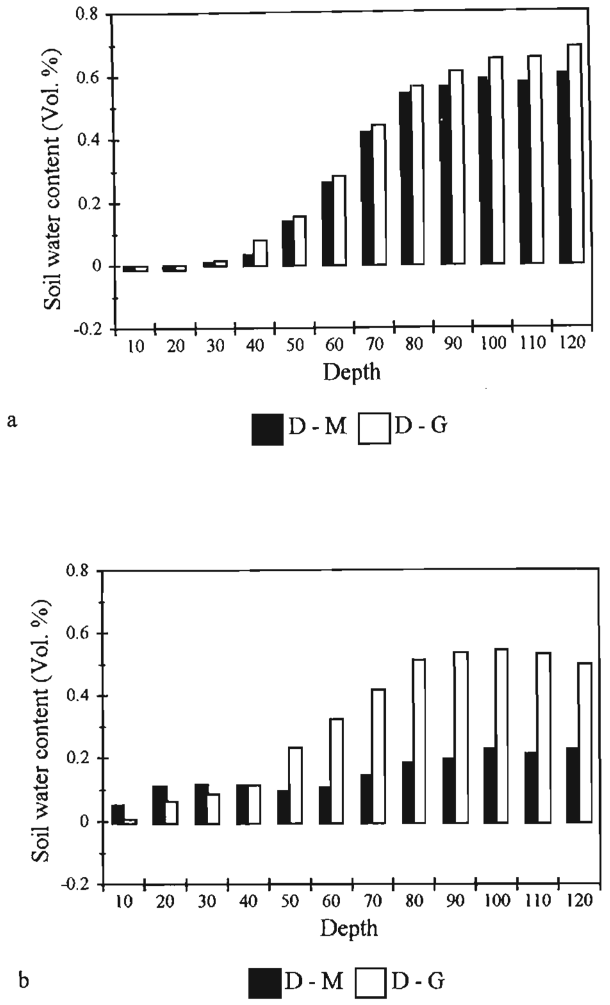
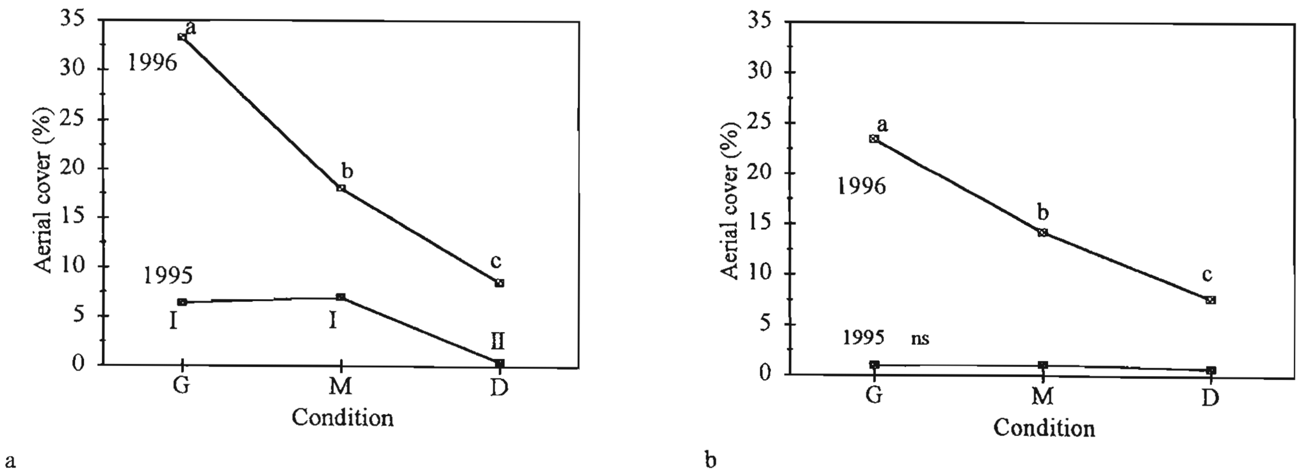


Figure 4.6 The difference in soil water content between degraded and medium condition rangeland (black bars) and between soil moisture content of degraded and good condition rangeland (white bars) (a) after a relatively long dry period (23 Oct 1995), and (b) one month after a recharge event (3 Jan 1996).

Both the number of annual (F=22.4, p<0.001) and perennial (F=10.5, p<0.01) species were significantly higher in 1996 than in 1995 (Figure 4.8b&c), and also differed with regards to rangeland condition (total number F=46.9, p<0.0001, annual species F=103.1, p<0.0001 and perennial F=18.6, p<0.0001). Furthermore, rangeland in different conditions responded differently to changes in rainfall (condition-by-year interaction) with regards to both the total number of species (F=10.7, p<0.01) and the number of annual species (F=11.3, p<0.01), but not for perennial species. The results of the decomposed models are indicated in Figure 4.8a,b & c.

Plant heights recorded monthly on the dune crest did not change significantly during the study period but were significantly different between condition classes (F=999.9, p<0.0001). The most abundant woody plant on the dunes, *Acacia haematoxylon*, covered a significantly (F=5.2, p<0.05) larger area on degraded dunes than on medium or good condition dunes (Figure 4.9).



a b

Figure 4.7 The influence of rangeland condition and rainfall (year) on (a) total vegetation cover and (b) annual vegetation cover. Between year differences were significant and differences within years between condition classes are indicated by letters.

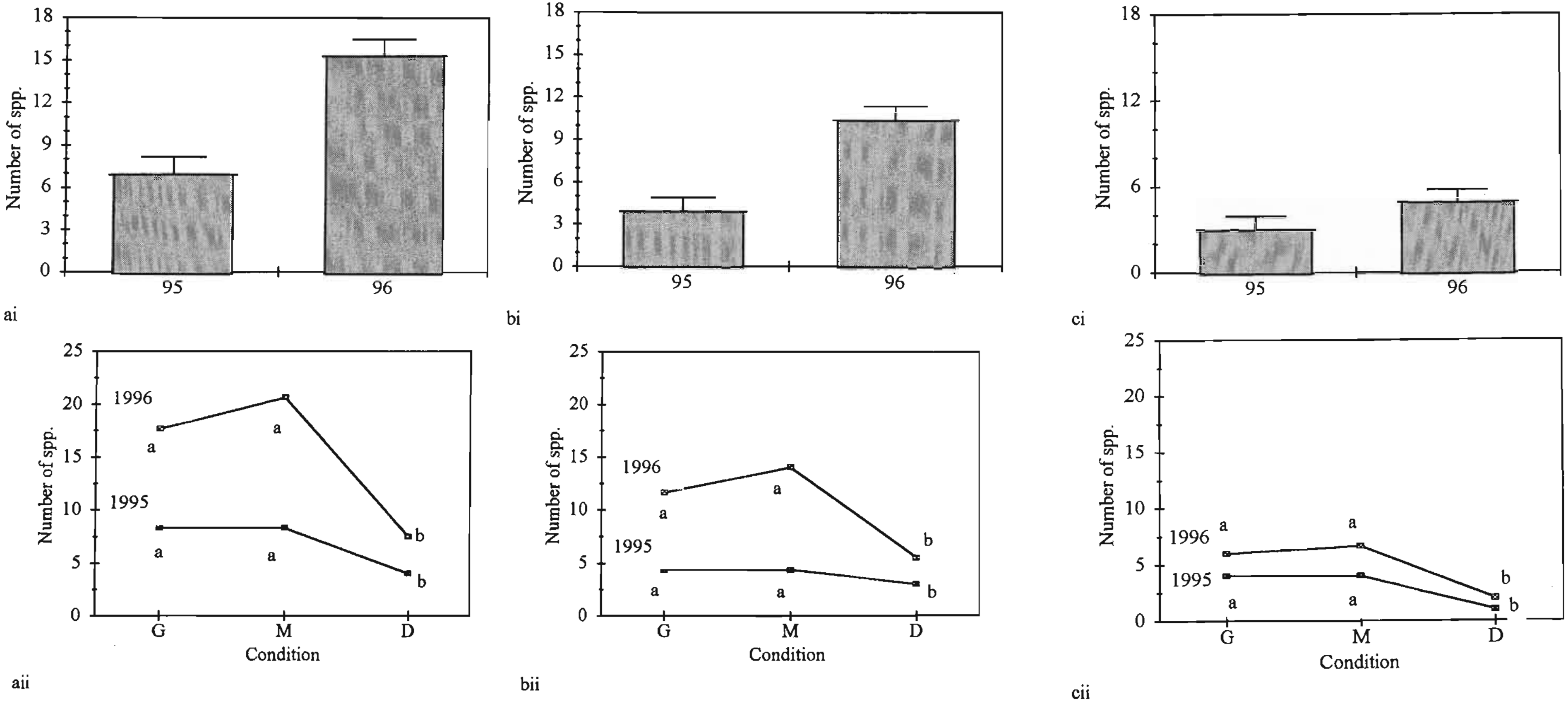


Figure 4.8 The influence of (i) rainfall and (ii) rangeland condition on (a) the total number of species, (b) number of annual species and (c) number of perennial species. Between year differences were all significant and differences, within years, between condition classes are indicated by letters.

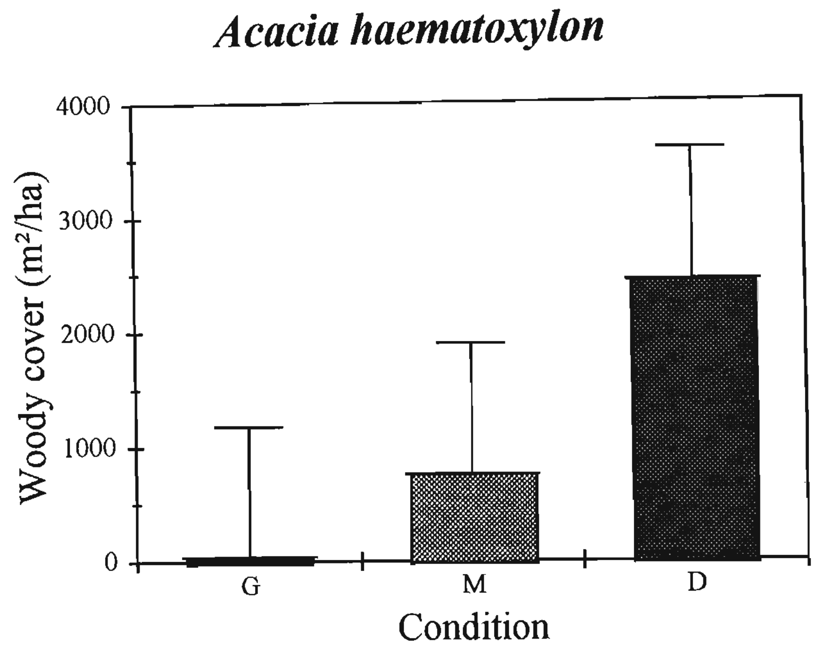


Figure 4.9 The aerial cover of *Acacia haematoxylon* in good, intermediate and degraded rangeland ($F = 5.21$ $p < 0.05$). Vertical bars represent 95% confidence intervals.

Discussion

Low rainfall during the initial stages of the study (until early Dec 1995, see Figure 4.1b) gave rise to fairly dry soil moisture conditions. Although relatively dry, soil moisture was different between the condition classes (Figure 4.2) and can be ascribed to differences in plant cover (Figure 4.7). Good condition dunes tended to be the driest during both the dry and wet seasons, which can be ascribed to their greater plant cover. There was no condition-by-depth interaction (Figure 4.3) during a relatively wet period, which suggests that moisture flow down the profile was consistent amongst condition classes. On the other hand, a significant condition-by-depth interaction during dry periods indicated that water extraction in medium and good condition dunes resulted in a soil moisture-depth profile different to that of degraded dunes. Moisture loss in degraded dunes is probably very rapid near the surface but ceases completely after the near surface layers are desiccated, and the only loss thereafter is through seepage to lower levels. The first basic conclusion from this study is thus that transpiration is the most important factor reducing soil moisture. This is further illustrated in Figure 4.4 where plant height and soil moisture were correlated at different depths. More moisture is taken up as the water column flows down the profile. The high correlations at the deeper levels does not indicate maximum root depth, as it is most probably only the result of less moisture reaching the lower levels.

The negative relationship between total soil water storage (S) and herbaceous plant cover has been experimentally illustrated (Link *et al.* 1994, Waugh *et al.* 1994). Moreover, the implication of this dynamic is well known amongst rangeland ecologists. Woody plants may increase as a consequence of high grazing pressure because of the resultant increased water availability to woody plants as herbaceous species are reduced (Noy-Meir 1982, Knoop & Walker 1985, Stuart-Hill & Tainton 1989, Skarpe 1990a, 1990b, Skarpe 1992). In the southern Kalahari, the dwarf shrub *Rhigozum trichotomum* has increased in the interdune areas as a result of high grazing pressure (Moore 1989). This study, however, dealt with moisture dynamics on southern Kalahari dunes, where, although the woody *A. haematoxylon* increased for the same reason, it never reached very high aerial cover (Figure 4.9). Moisture is rapidly used after rainfall events in good and medium condition rangeland but remains fairly high in degraded areas (Figure 4.5). In spite of this high moisture availability (Figure 4.3b(ii)), the large areas between trees remain bare for very long periods.

A conclusion would thus be that moisture availability is not a limiting factor for the recovery of vegetation in degraded areas. This raises a question as to whether a threshold exists where rainfall ceases to be the primary driving force in vegetation dynamics in this system? I suggested in chapter 3 that other factors (including: reduced nutrient levels and increased sand movement -

both consequences of reduced vegetation cover) could be responsible for the lack of recovery after degradation in the study area.

As in the Kalahari, Snyman and Fouche (1991) described reduced biomass production in degraded rangeland, but ascribed these differences to increased run-off and reduced infiltration, and thus reduced moisture availability. From Figure 4.7 and 4.9 it is clear that vegetation in different conditions reacts differently to the same amount of available water. Good condition vegetation shows a stronger response (significant condition-by-year interaction) to the available moisture, in terms of cover (an estimator of biomass). Changes in vegetation cover (and species) are minimal in degraded vegetation (Figure 4.8 and 4.9), while the response in terms of the number of species, to the same amount of rainfall is much greater in good and medium condition rangeland. Although more perennial species were encountered during 1996, perennial vegetation cover probably needs more than one season to improve significantly. It is thus clear that degraded vegetation did not respond to the relatively high rainfall of 1996.

Ironically, soil moisture is therefore not a limiting factor in the restoration of degraded Kalahari dunes.

Chapter 5

Using Landsat TM data to quantify rangeland degradation in the southern Kalahari

Introduction

Rangeland degradation impacts not only on biodiversity and primary productivity but ultimately affects the people who are dependent on the land. Detecting and quantifying rangeland degradation is particularly difficult in arid areas because of the high temporal and spatial variability of the vegetation (Bastin *et al.* 1993). Land-based techniques can determine changes in plant cover, diversity and productivity on a small scale, but extrapolating this information to the landscape level invariably results in uncertainties. The spatial nature of remotely sensed data and the relatively large areas that can be covered make it an attractive option to be used in concert with land-based information to map, quantify and monitor rangeland condition. However, as with land-based techniques, there are no universally appropriate techniques for interpreting remotely sensed data. The signal received by the sensor is determined not only by the vegetation but also by soil texture, colour and moisture content, the angle of incidence, shadows and an array of other site-specific variables (Tueller 1991). Most importantly, the amount of vegetation cover ultimately determines the accuracy and sensitivity of a technique.

Several vegetation indices have been developed for determining the quantity and quality of vegetation. These include most commonly the ratio-based techniques, of which the normalised differential vegetation index (NDVI) is most often used. Ideally in arid areas, such indices should be very sensitive to vegetation, insensitive to the soil background and only minimally influenced by atmospheric path radiance (Jackson *et al.* 1983). Consequently, indices have been specifically developed to deal with low vegetation cover in arid areas. Huete's (1988) soil adjusted vegetation index (SAVI) is but one such index.

One can not distinguish between plant species or vegetation types using remotely sensed data, therefore vegetation cover is the sole variable available on which to base evaluations regarding rangeland condition (Pickup *et al.* 1993). This results in complications regarding the use of remotely sensed data in the Kalahari, because the dunes and the interdunes react differently to disturbance (Chapter 3). Vegetation cover on the dunes is reduced during degradation while vegetation cover in the interdunes increases because of an increase in the annual grass *Schmidtia kalahariensis* (Chapter 3) and the shrub *Rhigozum trichotomum* (Moore 1989). Palmer and van Rooyen (1998) used change vector analysis (CVA, Michalek and Wagner 1993) to identify areas where rangeland changed between 1989 and 1994. Although this technique was suitable for the specific objective of determining directional change, it does not provide information regarding the detection and extent of previously degraded areas.

Quantifying degraded rangeland in the entire Mier area, using land-based techniques, would be time consuming and therefore not cost effective. Furthermore, the effect of the different land-use types in the area needed exploration to improve future decision making regarding land use options. The objective of this study was therefore to determine the potential of using remotely sensed data for identifying and quantifying degradation in the southern Kalahari, and for determining the effect of land use on rangeland condition.

Methods

Ground based vegetation data

For methods and general results see Chapter 3.

Remotely sensed data

Landsat TM scenes (bands 2,3 and 4) were obtained for the study area (full scene ID 175-0-078 940317). Images were taken at the end of the growing season and were geo-referenced in GRASS 4.1 (US Corp. of Engineers Research Laboratory, 1994) using pixel to pixel correction. Pixel size is 30m X 30m The Normalised Differential Vegetation Index (NDVI) was calculated using the standard NDVI algorithm provided by Idrisi (1995 Clark University, Graduate School of Geography).

On-ground sample sites were located on the images using a combination of aerial photography and GPS technology by making use of the dune structure, roads and farm boundaries, which were overlaid as a vector file. A polygon, including at least 25 pixels (thus at least 750m^2), surrounding a relatively homogenous area was drawn over each of the sites, using on-screen digitising. The QUERY function was used to extract the data pertaining to these sites from each of the three bands and from the NDVI image.

The average pixel value from the NDVI polygons were correlated with aerial plant cover (as an index of biomass), and eventually with the PCA (principal component analysis) model of the TM data to determine its validity as an index of rangeland condition in the southern Kalahari.

The data (excluding the NDVI data) from the polygons, in each band, were split in half, one half was used for the development of the model, and the second to test the model. The polygons were treated as sites and the average pixel values of the three bands were the response variables and analysed using PCA (CANOCO). The data was standardised and centred, to prevent any one band having a greater influence on the analysis. At first all data (dunes and interdunes) were analysed together. Subsequent analyses were done on dune and interdune data separately. To determine any relationship between the two models, the first PCA axis of the TM based data was then correlated with the first PCA axis of the on-ground vegetation data.

Once the TM degradation gradient had been verified, a new image was produced by using the three TM bands, centred and standardised, and weighted by the respective PCA 'band loadings' provided by CANOCO. This produced an image with each pixel containing its first $\mathrm{PCA}_{(\mathrm{TM})}$ score. This procedure provided a range of condition values from rangeland in good condition to degraded rangeland. In order to simplify interpretation of the resultant image, each pixel was reclassified into one of five categories, subjectively decided upon using the relationship between the first $\mathrm{PCA}_{(\mathrm{TM})}$ axis and plant cover. Three classes were used for the dunes, i.e. no or very little vegetation cover (0 - 12.9% cover), intermediate (13 – 15.9% cover) and high cover (16 – 21% cover), while the interdunes were divided into only two classes, i.e. low (22 – 27.9% cover) and high, >28% vegetation cover.

The repeatability of this procedure was determined by using the other half of the data from the polygons adjacent to the first set, on the assumption that species composition and cover of the data are comparable. The $\mathrm{PCA}_{(\mathrm{TM})}$ axis 1 scores of the 56 polygons of the second set was calculated and then classified into five classes. Both data sets were classified using the same class intervals and compared.

To illustrate the influence of the different land-use types on rangeland condition, the total area of land in each condition class was calculated for a section of the Kalahari Gemsbok National Park; the game ranches: Pulai and Campspannen; and a stock farm, using standard GIS procedures. In addition, to illustrate the difference in the spatial effect of domestic stock and indigenous herbivores on rangeland condition regression analysis of the distance from a waterpoint and the $PCA_{(TM)}$ scores of two different farms were done. For this exercise, Campspannen, a game ranch, and a domestic stock farm was used. This was achieved using the 'distance' algorithm in IDRISI to produce images where each pixel number was the distance from the nearest waterpoint. These images were then regressed against the respective $PCA_{(TM)}$ images of the two farms. The total area available to grazing, on each farm, was calculated using the same procedure. Linear regressions were done using Statgraphics 5 while multivariate analysis was done using CANOCO. GIS analysis was done using IDRISI 1 for Windows.

Results

There is a significant negative correlation between the aerial plant cover and the average NDVI values from the polygons, which overlapped the sites where on-ground vegetation data was collected (Figure 5.1a). Inspection of the NDVI image also illustrates high NDVI values associated with bare soil in piospheres (plate 5.1).

A biplot of the first and second axis of the $PCA_{(TM)}$ revealed that the dunes are generally on the negative side of the first PCA axis while the interdunes are on the positive side (Figure 5.2). The eigenvalue of the first $PCA_{(TM)}$ axis is 0.622, whilst that of the second is only 0.001. The first axis was thus by far the most important 'new' variable, because it contains the greatest amount of combined information. Band two (B2) and band three (B3) made a greater contribution to the PCA ordination than band four (B4), while there is a greater correlation between B2 and B4 than between B3 and B2 or B4 (Figure 5.2). Therefore there were very good correlations between both B2 and B4 and the first PCA axis, while B3 also correlated significantly with the first PCA axis, but the r-value was lower (Table 5.1).

Table 5.1 Linear correlation between the first $PCA_{(TM)}$ axis and other variables.

	$PCA_{(TM)}$ Axis 1
Band 2	-0.950****
Band 3	-0.805****
Band 4	-0.884****
Aerial herbaceous cover	0.627****
Woody cover	ns
Organic Matter	0.746****
Total P	0.574****
Available P	0.538****
Total N	0.693****

There is a significant linear relationship between plant cover and the first $PCA_{(TM)}$ axis (Table 5.2). Because the dunes and interdunes were separated on the first $PCA_{(TM)}$ axis linear regressions on the plant cover of the dunes and interdunes were done separately (Figure 5.3).

Although the y-intercept of the interdune data may be lower than that of the dunes, the slopes of these relationships were not significantly different. Similarly, OM, total nitrogen and total and available phosphorous were significantly correlated with the first PCA$_{(TM)}$ axis (Table 5.1). There was no relationship between woody plant cover and any of the PCA$_{(TM)}$ axes.

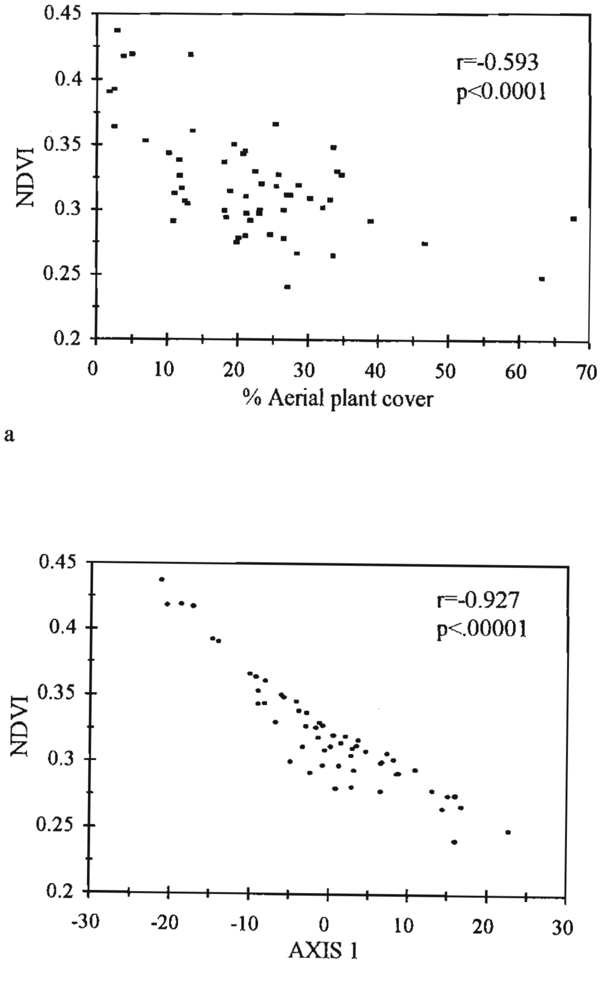


Figure 5.1 (a) The relationship between aerial plant cover and the Normalised Differential Vegetation Index (NDVI). (b) The relationship between the NDVI and the first PCA$_{(TM)}$.

Table 5.2 Linear correlations between the first $\text{PCA}_{(TM)}$ axis based on the average reflectance in polygons (ranging between 25 and 50 pixels) covering the 28 surveyed dunes and interdunes of TM bands 2,3 and 4 and PCA data of the same sites based on species cover data. Correlations between the TM data axis and other important variables are also indicated. See text for further details.

	$\text{PCA}_{(TM)}$Ax1 Dune	$\text{PCA}_{(TM)}$ Ax1 Interdune
$\text{PCA}_{(Spp)}$ (log)	0.664***	0.469*
Disturbance		
Current grazing	Ns	ns
Historical grazing	-0.479**	ns
Disturbance coefficient	-0.501**	ns
Vegetation		
Total Cover	0.737****	0.509**
Height	0.859****	ns
TM Data		
Band2	-0.976****	-0.877****
Band3	-0.849****	-0.584**
Band4	-0.929****	-0.795****

(*: $p < 0.05$; ** $p < 0.01$; ***: $p < 0.001$; ****: $p< 0.0001$)

The next objective was to test whether there was a relationship between the first PCA axis derived from the TM data and the first PCA axis derived from the on-ground vegetation data. The first $\text{PCA}_{(TM)}$ axis scores of the dunes and interdunes correlated significantly with their respective $\text{PCA}_{(Spp)}$ scores (Table 5.2). In addition the $\text{PCA}_{(TM)}$ scores for the dunes also correlated with the historic grazing pressure and the disturbance coefficient (Table 5.2). The first $\text{PCA}_{(TM)}$ axis was significantly correlated with herbaceous aerial plant cover. Plant height, on the dunes only, was also well correlated with the first $\text{PCA}_{(TM)}$ (Table 5.2).

When evaluating the repeatability of the classification of the sites into condition classes, it was found that only ten of the 56 sites were wrongly classified, 82% of the sites were thus correctly classified (Table 5.3). The actual accuracy may be higher because the two halves of the polygons were only assumed to be the same. In addition, all divisions between classes, except the division between classes 3 and 4, were arbitrarily made along a linear continuum. Small differences at the borders of these classes can thus bring about some inconsistencies. Two dunes and two interdunes were incorrectly classified as interdunes and dunes respectively (Table 5.3).

Table 5.3 Testing the repeatability of the method using the second data set. The number of sites from the first data set are listed in the different classes together with the number of sites incorrectly classified using the second data set.

Classes	Data set 1	Data set 2 Classified as a class: lower	 higher
1 Dunes: bare	6	0	0
2 Dunes: low cover	7	0	2
3 Dunes: high cover	15	2	2
4 Interdunes: low cover	20	2	1
5 Interdunes: high cover	8	1	0
	56	5	5

The contribution of the various condition classes differs between the management units investigated (Table 5.4). Almost completely bare areas (class 1) constituted 16 and 19% of the overgrazed game ranch Pulai and the stock farm respectively, compared with 3% of the conservation area and 7% of the game ranch in relatively good condition (Campspannen). In support of this, all the sites from Pulai and Campspannen were consistently classified near the degraded and good condition ends of the degradation gradient (Chapter 3) respectively.

Table 5.4 The proportion of land in each of the condition classes of a formal conservation area (KGNP), a degraded game ranch (Pulai), a game ranch in relatively good condition (Campspannen) and a small stock farm. (See Plate 5.2 for locations.)

Category	Cover %	Total Area Ha (%)	KGNP Ha (%)	Pulai Ha (%)	Campsp Ha (%)	Stock Ha (%)
Dunes						
1: bare soil	0 -12.9	6.63	3.14	18.60	6.75	16.39
2: low cover	13-15.9	28.91	23.43	13.23	18.72	22.82
3: high cover	16- 21.9	27.36	26.28	15.40	20.23	18.61
Interdunes						
4: low cover	22-27.9	28.67	34.74	36.61	37.14	29.89
5: high cover	28<	8.43	12.41	16.16	17.16	12.29

The area of rangeland in classes 2 and 3 on Pulai were low compared with the average of the entire area. It is, however, important to note that, although the total area of rangeland in class 1 was similar in the stock farm and in Pulai, the spatial distribution thereof was remarkably different (Plate 5.2). Furthermore, the effect of water holes (piospheres) were very clear in the stock farming areas (southern areas of the image, Plate 5.2, Figure 5.4), whereas no such effect was evident in the northern areas of the image where indigenous game species were the only herbivores. The relative area available to herbivores on both farms, in relation to the distance from water, was similar (Figure 5.5). This indicates that although domestic stock had access to a similar area (in size), these areas were not utilised by them. Indigenous species are far less dependent on water and can therefore forage and utilise resources further afield from water than domestic stock.

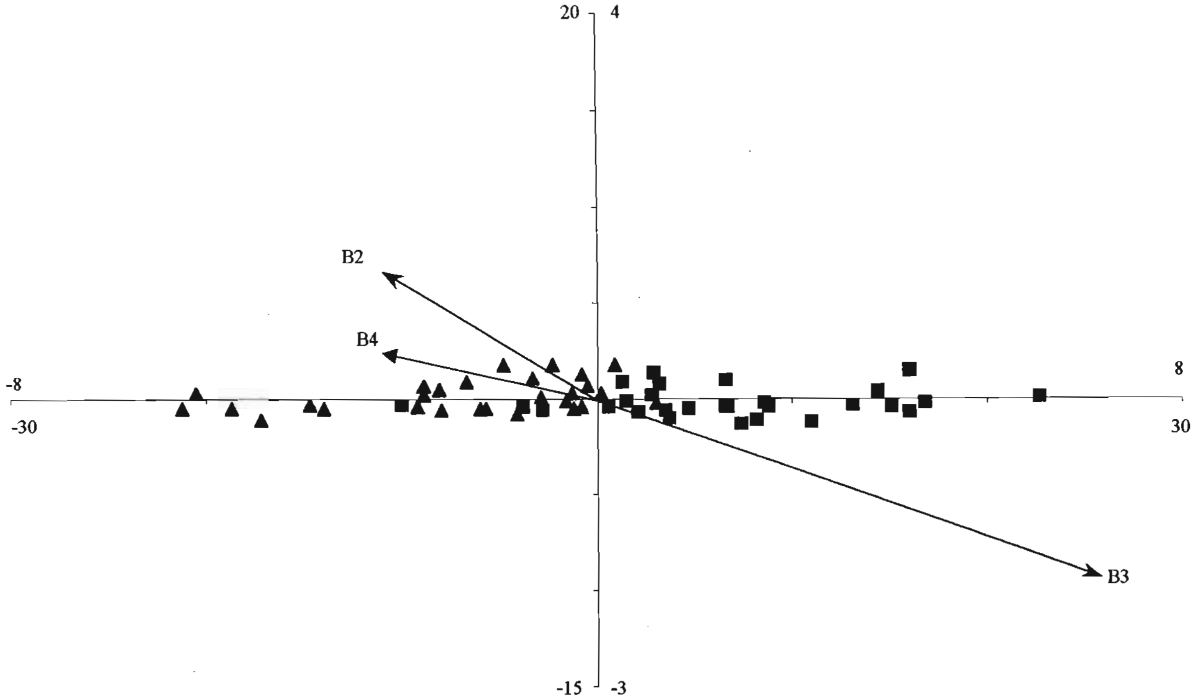


Figure 5.2 The PCA biplot of the TM bands and sites (▲ dunes; ■ interdunes) of the average pixel values in polygons covering areas where on-ground vegetation sampling was done. Eigen values were 0.622 and 0.001 for the first and second axis respectively.

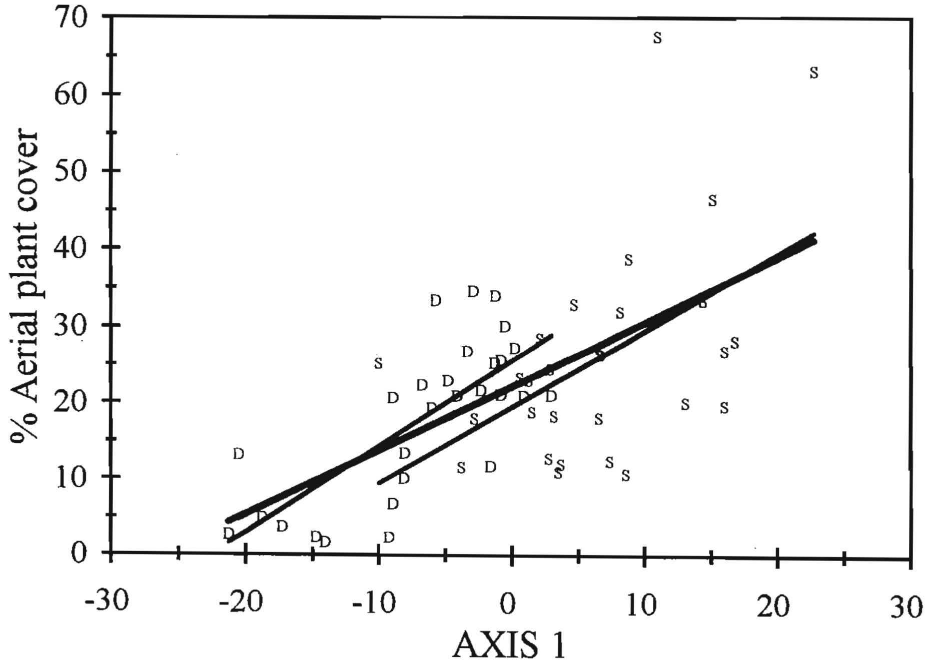


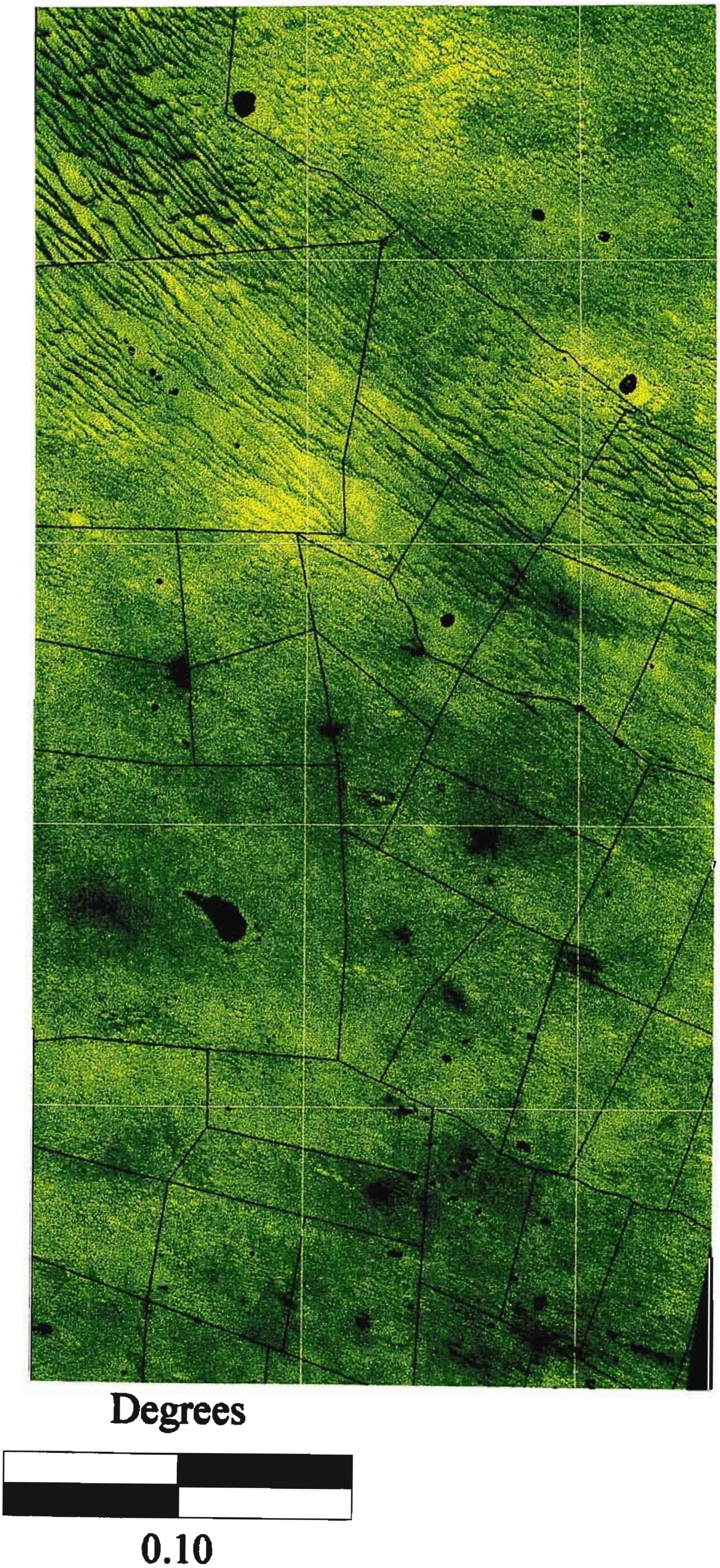
Figure 5.3 The relationship between aerial plant cover and the first PCA$_{(TM)}$ axis (D = dunes, S = interdunes). The short lines on the left and right represents the plant cover on the dunes and interdunes respectively, while the long thick line represents the entire data set.

Plate 5.1 NDVI of the north-western section of the Mier area. Note that very high NDVI values are bare red soil in the centre of piospheres and bare dunes in highly degraded areas.

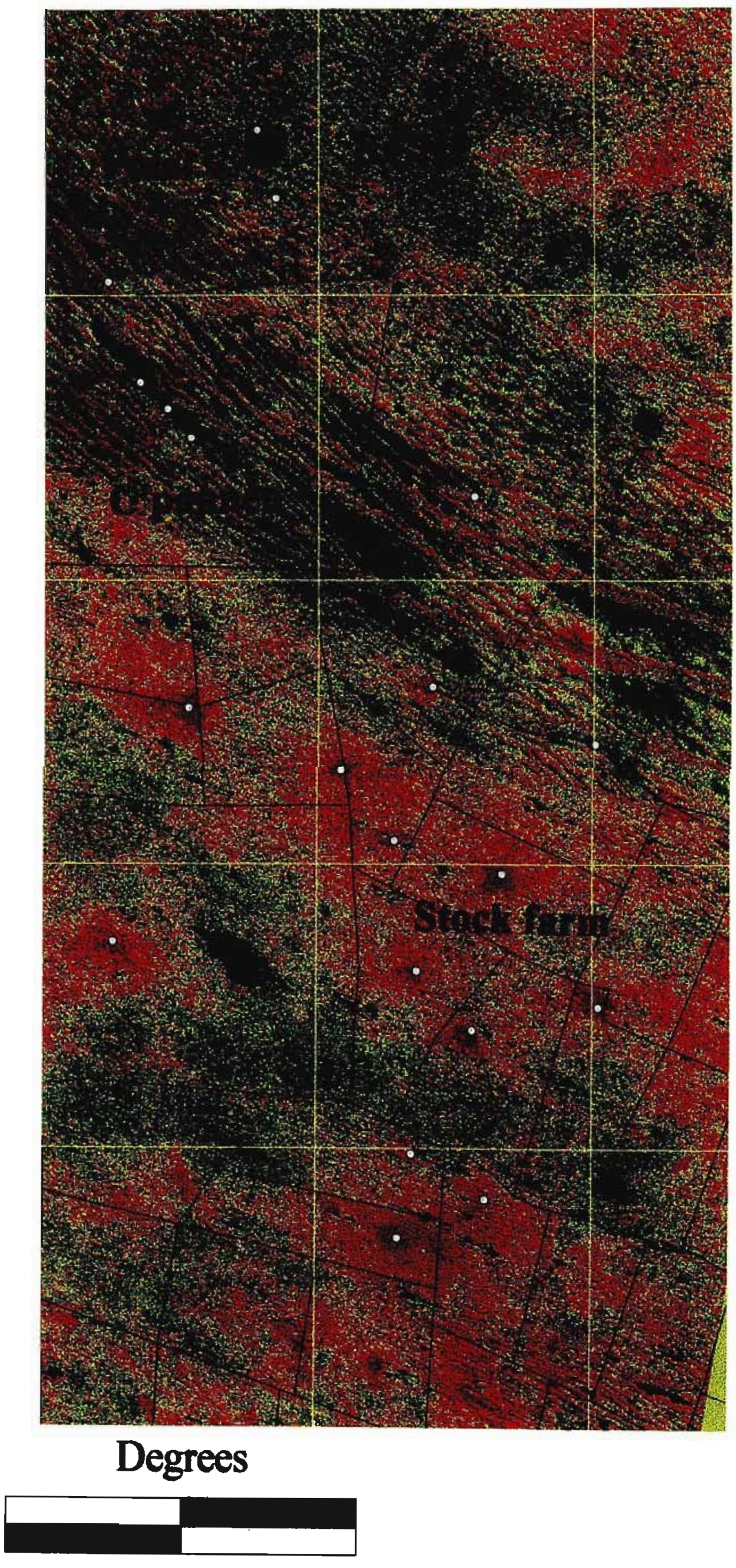
Plate 5.2 **A reclassified image of the north-western section of the Mier area, based on the calculated first PCA axis of polygons covering the on ground vegetation sampling sites.**

Category	Cover %	Class	
Pans	0	0	⬛
Dunes: Bare soil	0 -12.9	1	🟥
Dunes: Low cover	13-15.9	2	🟥
Dunes: High cover	16- 21.9	3	🟨
Interdunes: Low cover	22-27.9	4	🟩
Interdunes: High cover	28<	5	⬛
Fences			—
Boreholes			○

NW Mier: NDVI 1994



NW Mier: Recl. PCA 1994



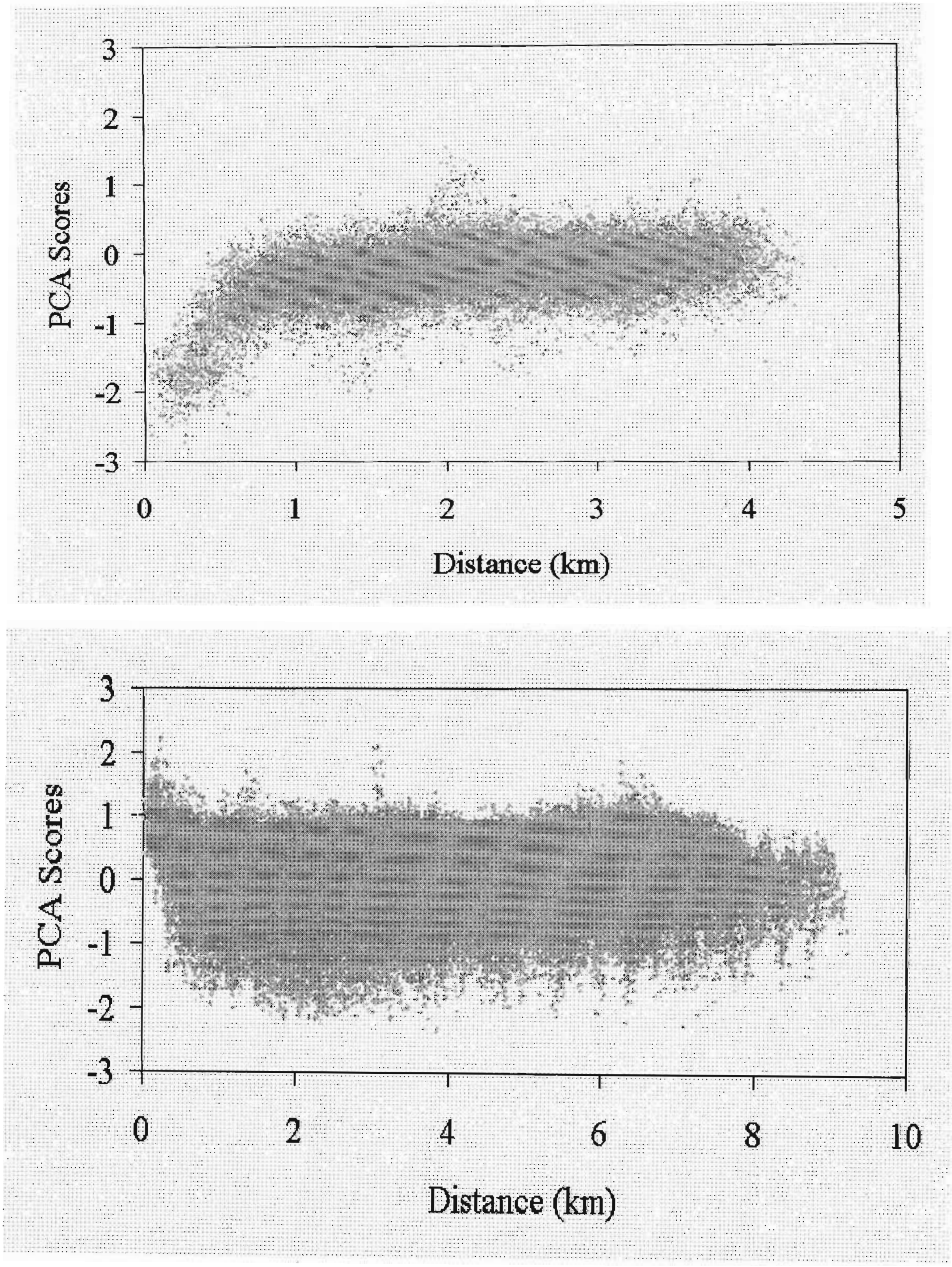


Figure 5.4 The relationship between the distance from a water point and the $PCA_{(TM)}$ scores. (a) Domestic stock farm with sheep and goats as the dominant herbivores. (b) A game ranch (Campspannen) with springbok and gemsbok as the dominant herbivores. (See Plate 5.2 for locations.)

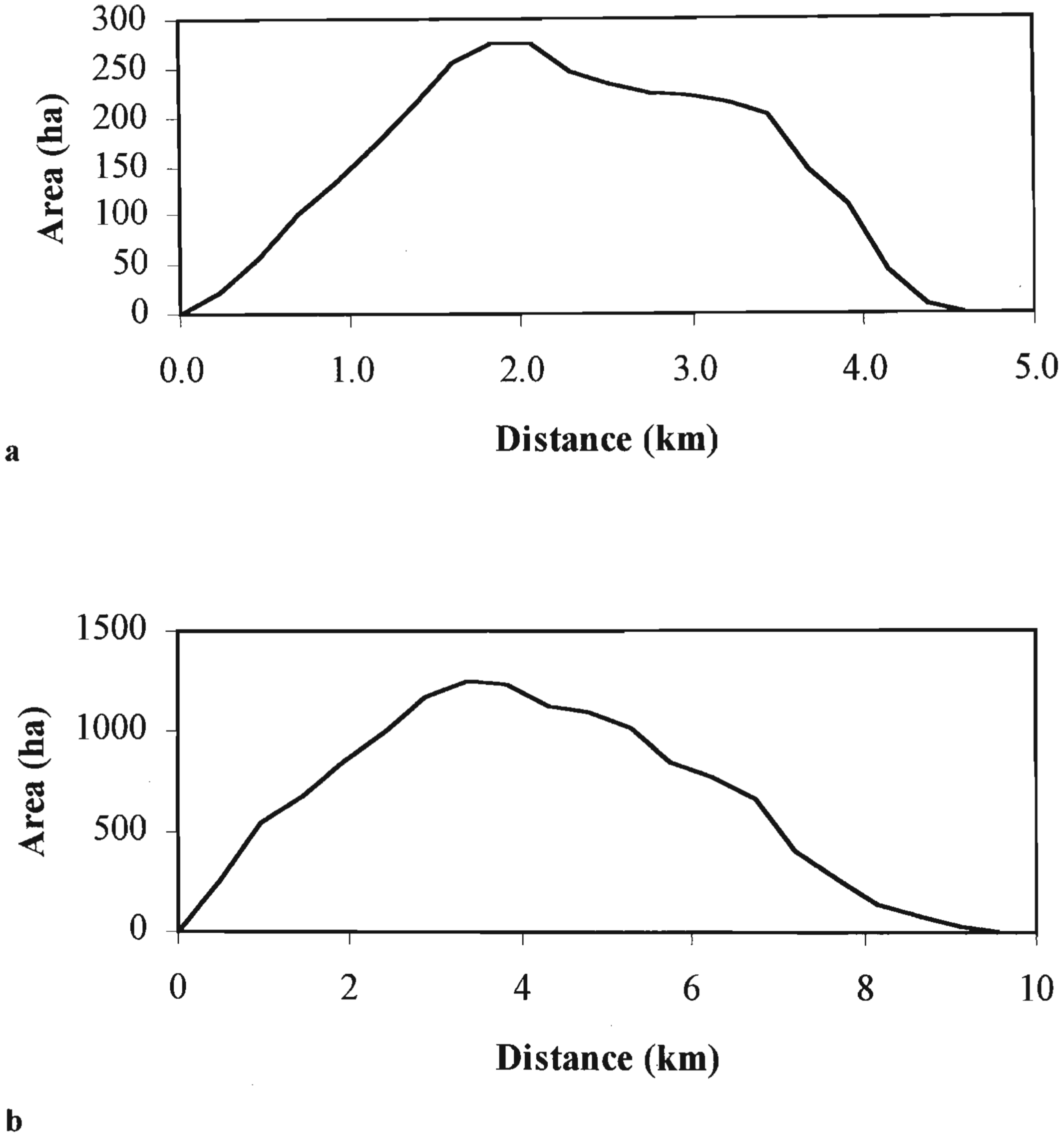


Figure 5.5 The area (ha) available to grazing radiating from the water points on (a) the stock farm and (b) the game ranch.

Discussion

The southern Kalahari is known for its red sand dunes. This red colour is the result of an iron oxide coat around the quartz grains. Consequently, TM4 has very high reflectance values for pixels covering bare soil in the Kalahari. Rationing indexes such as the NDVI do not therefore provide accurate information regarding plant cover or biomass. Ground-based estimates of herbaceous plant cover showed a negative relationship with NDVI (Figure 5.1a) and, although NDVI had a strong negative relationship with the first $\mathrm{PCA}_{(\mathrm{TM})}$ axis, its information content with regard to vegetation cover remains low (Figure 5.1b) . Although the index is not of no value, as it still contains important information once verified with ground data, the relationship is in stark contrast with that in other areas. The NDVI's relevance in arid areas with predominantly red soils is inconsistent with other areas and is therefore limited. Pickup *et al.* (1993) also found a negative correlation between NDVI and vegetation cover, and also discarded the index because of its weak relationship with vegetation cover.

Ground-based vegetation data (cover and species composition) are often subjected to multivariate statistics in order to reduce the number of variables to a much smaller number, which are interpreted using simple graphing techniques. As part of this study, several sites covering a wide range of visually different vegetation states were surveyed and analysed using PCA to define a degradation gradient (Chapter 3). This gradient, $\mathrm{PCA}_{(\mathrm{Spp})}$ axis 1, has been confirmed as it correlated significantly with plant cover, soil particle size, OM, P and nitrogen (Chapter 3). The same methodology was used to develop a comparable gradient but using the three different TM bands as variables. With the on-ground vegetation data, dunes and interdunes separated along the first and second $\mathrm{PCA}_{(\mathrm{Spp})}$ axis and were therefore subsequently analysed separately. However, although possible while building the model using the polygon data, both dunes and interdunes would need to be included in the final model. Therefore data from both the dunes and interdunes were included in the $PCA_{(TM)}$.

The positive relationship between vegetation cover, OM, total N, total P, available P and the first $PCA_{(TM)}$ (Table 5.1) also confirms the validity of the axis as a gradient from low to high nutrient status (or potential ecosystem functioning). There is, however, the aforementioned discrepancy. Interdunes in good condition have lower aerial plant cover than degraded interdunes, because *S. kalahariensis* and nutrient levels increase in degraded interdunes as nutrients are lost from the degrading dunes (Chapter 3). The negative side of the $PCA_{(TM)}$ axis is a gradient ranging from bare dunes on the left to dunes with high cover near the origin, then the gradient is reversed for the interdunes, going from good condition interdunes (with relatively low cover) at the origin to degraded interdunes on the far right (with high vegetation cover). The reclassification of this data, to separate dunes from interdunes, and to divide dunes and interdunes into cover classes, bridges this anomaly by creating two cover based indices inter-spaced as a mosaic on a single image.

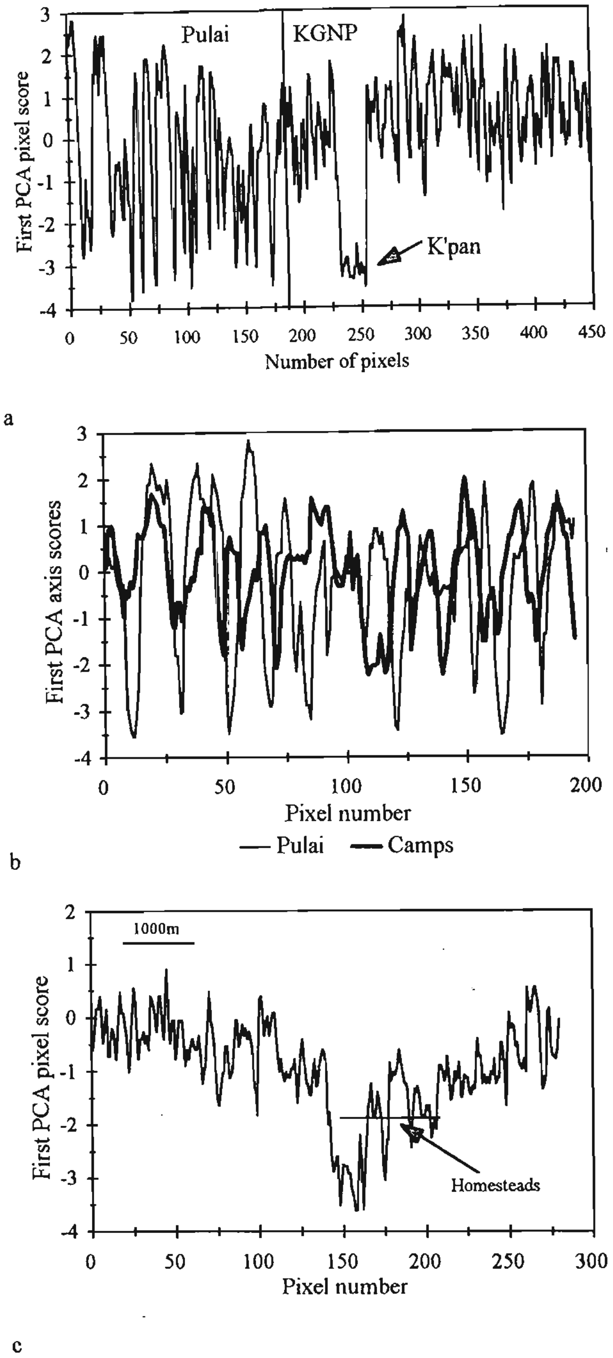


Figure 5.6 A series of graphs illustrating fence line contrasts (a&b) and the effect of homesteads (c) on rangeland condition in the southern Kalahari. . The pixel values are the $PCA_{(TM)}$ values calculated for the entire image from the results of the PCA using the polygons covering individual sampling sites. Pixels are 30x30m squares. (a) A 'transect' across the degraded ranch Pulai, and the Kalahari Gemsbok National Park (KGNP), K'pan, in the KGNP is a bare calcrete pan. (b) Two parallel transects on either side of the Pulai/Campspannen fence. (c) A transect through the Keikwas homestead complex. A few homesteads with their associated kraals and water points have denuded a large area of dunes.

The level of accuracy obtained is regarded as acceptable on the landscape level (Table 5.3). In addition, both the interdunes that were wrongly classified were on very deep sand with species composition and cover values comparable to that of dunes. Furthermore, these sites were all located in a section of the study area with a dune structure different from the rest of the study area. The dunes are not consistently linear, and were classified as class 4 dunes, described as a linear dune network with well vegetated interdunes which are not as clearly defined and of variable depth (Bullard *et al.* 1995).

Detection and quantification

Figure 5.6a illustrates the pixel values of a transect (one pixel wide) from inside the degraded game ranch, Pulai, across the fence and a large calcrete pan and into the Kalahari Gemsbok National Park. It is clear that the conservation area has higher vegetation cover than Pulai, and that the dunes in Pulai are just as bare as the calcrete pan. The method developed is thus not only capable of quantifying vegetation cover, but can, at a larger scale, illustrate differences between land use types with regard to the spatial distribution of impact (Figure 5.6).

Although a continuum of values describing rangeland condition ($PCA_{(TM)}$ axis 1), as a spatially explicit data set, is ecologically more appropriate, dividing it into different condition classes allows for simplified interpretation. Describing a ranch (or other management unit) in terms of it's composition per unit area of each of the condition classes allows for direct comparison between farms and potentially also on a temporal scale. Furthermore, classes close to the degraded end of the continuum may be regarded as being in a vulnerable state. In case of this study it will be the dunes with low vegetation cover. Table 5.4 provides surface areas of four different management units in categories ranging from bare areas (totally degraded including pans and roads), deep sand with low and high vegetation cover (essentially dunes) and interdunes with low and high vegetation cover. The proportion of bare ground in the KGNP and on the relatively well managed Campspannen is relatively low, while it is high on the previously heavily grazed ranch, Pulai, and the small stock farm. The opposite is true for the proportion of land with high vegetation cover (good rangeland) on deep sand. Pulai and the small stock farm have only 15 % and 18 % of the rangeland in this category while the KGNP and Campspannen have much larger areas in this category. Compare these figures with the average of the entire area (Table 5.4). It is important to note the interdunes of the these areas are in similar condition. This is most probably a result of the interdunes being more vulnerable to degradation than the dunes (see Chapter 3).

It is important to note that averaging an entire management unit to express condition as a single figure will not be accurate. Two transects on either side of the Campspannen/Pulai fence illustrates this clearly (Figure 5.6b). The bare dunes in Pulai result in low $PCA_{(TM)}$ scores, while it is higher in Campspannen because of higher vegetation cover. The average pixel values (1.25 and 1.19) for the two transects are not markedly different, but their standard deviations (1.5 and 2.8) are clearly different.

The influence of land-use

Three main forms of land use occurred in the study area, of which two, the conservation area and the game ranches, are very similar with regard to the type of herbivore that utilises the area. Even a very superficial visual inspection of Plate 5.2 will indicate the difference in the pattern of degradation between the game areas in the northern section of the image, and stock areas in the southern section of the image. In all of the stock farms, the central *point of activity* is clearly visible. This is in most cases the homestead complex from where all farming activities take place. In most cases it also contains the only water point on the farm, and all animals are normally kraaled there at night to reduce predation by jackal (*Canis mesomelas*). These piospheres are clearly visible in the reclassified $PCA_{(TM)}$ image (Plate 5.2, see also Figure 5.6c). Those factors and characteristics that can potentially lead to such a difference in the spatial impact of domestic stock and indigenous game species are listed in Table 5.5. From the evidence provided here, indigenous species, especially water-independent game species, such as gemsbok *Oryx gazella* and springbok *Antidorcas marsupialis* have a lesser impact on the rangeland than domestic stock. However, based on the evidence in Pulai, where game was concentrated during the development of the Mier area, heavy grazing by wildlife can have landscape wide consequences (see Figure 5.6a).

Table 5.5 The characteristics of stock and game ranching that can lead to a difference in the spatial pattern of impact of these land-use types.

Domestic herbivores	**Indigenous herbivores**
Temporal variation in numbers	
Although domestic animals are not as well adapted to arid areas, their numbers are often artificially kept stable through droughts by supplementary feeding and imports once conditions improve. Although predation cause great distress to stock owners, it does not act significantly as a factor reducing population numbers, mainly because stock are often kraaled at night.	Game species are often significantly affected by forces that limit or regulate populations. Droughts, especially in fenced areas, can reduce populations dramatically and recovery time is long. Variation in game numbers are thus often of much higher magnitude than for stock numbers.
Human Behaviour	
Domestic stock's behaviour is modified by the stock manager. Animals are artificially concentrated at various places. Population dynamics are modified by managers, by artificial reductions and imports and sex ratios are skewed.	Human influence on indigenous herbivores behaviour is limited and if anything it tend to disperse animals.
Species differences	
Concentrated around points of attraction, ie water, licks, kraals etc. Domestic stock are highly dependant on water and are specifically selected for protein production, being very effective converters of forage to protein. Animals tend to be more sedentary and movement over the landscape is determined largely by the stock manager.	Springbok and gemsbok are largely independent of water and are well adapted to the environment and the available forage species, including a wider range of species in their diet. They tend to be more mobile, utilising a much wider range of habitats.

Conclusions

NDVI correlates negatively with rangeland condition and indices of biomass, such as aerial cover and plant height. The results obtained from this technique in the study area are therefore inconsistent with that in mesic areas. The method employed here; the development of a condition surface using PCA of on-ground data of specific sites, and the verification of this surface by comparison with ground-based data, may not be a quick fix, but a reliable rangeland condition surface (with confidence limits). Furthermore, this “condition” image can be calculated for the dunes and interdunes respectively and both can be presented on a single image. The contribution of condition classes per unit area within different management units can be calculated for management and monitoring purposes. The technique is accurate enough to distinguish between dunes and interdunes, the different forms of land use, and the data clearly illustrate the spatial variation of rangeland degradation in the southern Kalahari. Further work needs to be done to investigate the temporal application of the technique and the apparent insensitivity of the technique for the woody component.

Chapter 6

Aspects of *Stipagrostis amabilis* and *S. ciliata* population dynamics in degraded Kalahari rangeland

Introduction

Very little is known regarding the population dynamics of any of the grasses in the southern Kalahari. In an attempt to determine the potential colonisation rates of *Stipagrostis amabilis* and *S. ciliata* on degraded dunes, various aspects of the population dynamics were studied. Both these species occur in small, low lying (protected) patches on degraded dunes in the study area.

Stipagrostis amabilis is a rhizomatous or tufted grass, growing on dune crests or in other areas of deep sand (Gibbs Russel *et al.* 1991) and plays an important role in stabilising dunes. Lateral tillers arise from nodes typically near the roots but secondary tillers are often produced from the nodes of older tillers. Where long tillers touch the soil they may root, but this happens only very occasionally. In the study area it occurs in a range of 'growth forms' from sparse individual tillers to large (1-4m circumference) clumps, often on 'pedestals', which are the result of the surrounding sand being eroded. *Stipagrostis ciliata* is a palatable, tufted grass, which is under 'normal' conditions associated with interdune areas with deep sand. Discrete individual tufts are well spaced and easily recognised. Seedling establishment is the usual origin of a new tuft. Although *S. ciliata* usually occurs in the interdunes, their natural ability to establish and colonise the degraded (flat) dunes, stimulated interest in this species. Not only would information regarding the dynamics of these species facilitate our understanding of the dynamics of the southern Kalahari, but it would also indicate the potential of these species to be used in restoration efforts.

Another aspect that requires investigation is the spatial and temporal scale at which ecological processes occur. This has been reported as a crucial consideration for rangeland monitoring (Friedel 1994). The effective monitoring of rangeland, to detect changes in species composition and cover, is often restricted by the small scale of operation and the consequent inability to extrapolate observed information to the level of the landscape. In this chapter I argue that the opposite is often also true. Small scale changes (at the level of the individual or patch) are often overlooked because the scale of operation, that aims to detect landscape level changes, is ineffective at identifying such small but significant changes. Rangeland monitoring often aims at providing data to develop early warning systems. Detecting changes at the landscape level would indicate that changes at this level have already taken place, and could thus hardly be used as a stimulus for reaction with regard to adaptive management.

The organisational levels commonly recognised by ecologists are: organism, population, community, ecosystem and landscape (Brown and Allen 1989). These levels of scale have been described as somewhat arbitrary because they depend, in this case, on the objective of the monitoring programme or, more generally, on the way in which it is observed. Senft *et al.* (1987) used a similar hierarchical arrangement: plants, micro-patches, communities or large patches, landscape and region. Friedel (1994) highlighted the importance of the distinction made by Brown and Allen (1989) between the categories of organism, population and community on the one hand, and region, ecosystem or landscape on the other. The first group is organism or taxon based and is concerned with (living) aspects such as population dynamics, while the other, ecosystem and landscape, is concerned with the processes such as energy and nutrient flow. Friedel (1994) clearly demonstrated that the spatial and temporal scale and distribution of ground-based monitoring will determine whether the community/landscape is perceived as degrading or not.

This study investigates such a case. Recovery at the landscape level of degraded southern Kalahari rangeland is considered either as non-existent or at a rate too slow for the time frame at which the landowner operates. The negative feedback mechanisms that operate at this level (chapter 3) supports this notion. This information does not, however, encompass lower level processes, and casual observations indicated that the aforementioned species increase in numbers in small, localised patches. Although these observations at the organism or plant (and population) level were in stark contrast with the landscape-based information base, the two data sets are by nature not directly comparable. These apparently contradictory observations stimulated investigation into the potential recovery of degraded rangeland at the lower levels of organisation.

The objectives of this study were thus to determine the fate of individual tillers and tufts of *S. amabilis* and *S. ciliata* at the patch level. Furthermore a demographic study could potentially indicate factors and processes that determine population dynamics which would indicate the direction and magnitude of change. The final objective is to attempt to link and interpret the results from the two levels of investigation.

Methods

Stipagrostis amabilis

Populations of tillers, from the two extreme growth-forms mentioned, as well as an 'intermediate form', small 'tufts' originating either from seed or rhizomes, were monitored. At a particular site, two sample populations were selected, one which was protected from grazing by large mammalian herbivores, and the other left open to all herbivores. Sample sizes per site were not equal as a result of the uneven distribution of the different forms: n=4 for the clumps, and 2 each for the sparse tillers and smaller tufts. The response variables also differed between the different forms. For the sparse and clumped populations, individual tillers were marked and the number of aerial tillers was counted. For the smaller tufts, the number of tufts within a clearly demarcated area was counted, as well as the number of tillers which carried aerial tillers. Young tillers, without aerial tillers, were ignored because of potential observer bias in establishing the number of tillers and to determine which tillers were alive or not. Tillers with inflorescences and grazing were recorded. Monitoring took place at approximately 60 day intervals from March 1995 until June 1998.

Stipagrostis ciliata

At least 50 individual tufts in each of four different patches were demarcated and each plant permanently marked using numbered steel pegs. These patches were typically a few older, isolated tufts, surrounded by younger plants, most probably their offspring. Plant height and circumference were measured to the nearest cm, the number of seed-bearing inflorescences was counted and plants were inspected for fresh evidence of grazing. To assess plant vigour, the proportion of dead tillers in a tuft was estimated to the nearest 10%. The relative height of the soil surface to the plant was classified into 5 erosion classes: -1 to –3 for slight to severely eroded plants; 0 for no erosion and 1 for a tuft which base is at least partially covered with sand. The sampling interval was approximately 60 days, which started in March 1995 and ended in January 1998. All seedlings were marked with numbered steel pegs. The size of exclosures required, and the problems pertaining to the sandy surface for protecting a large enough sample of tufts from large herbivores, prevented grazing from being included as a variable to be tested.

Results

Stipagrostis amabilis

There were no significant differences between open and protected *S. amabilis* populations with regards to any of the variables investigated (i.e. total tiller number, aerial tiller number and tiller birth and death rates). Where *S. amabilis* occurs as loosely spaced individual tillers (Figure 6.1), tiller number per unit area increased in reaction to higher soil moisture levels (Figure 6.7(a)) after the rainfall events during Dec 1995. Thereafter, tiller density decreased slowly to reach levels comparable to that during the driest period of the study (Nov 1995). The average number of aerial tillers (used as an index of tiller vigour) also increased in reaction to rainfall, but remained high at the end of the study. Tiller density of *S. amabilis* in this 'growth-form' may thus be at an optimal density and is probably controlled by soil moisture (rainfall).

The number of tillers in demarcated areas on the edge of large *S. amabilis* clumps increased markedly during the year following the rains of Dec 1995 (approximately

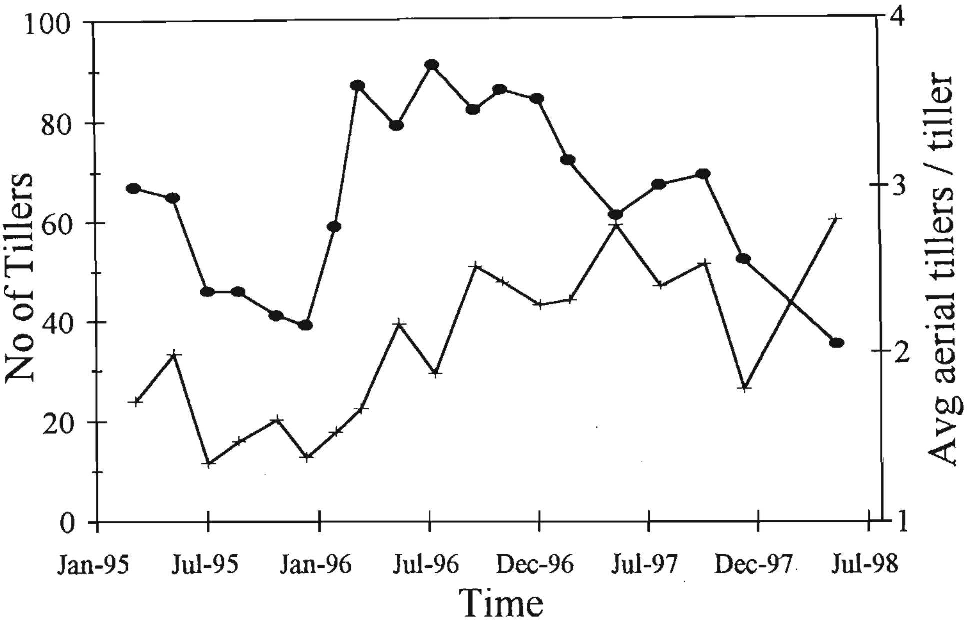


Figure 6.1 The number of rooted (●) and aerial tillers (+) in a population of loosely spaced individual *Stipagrostis amabilis* tillers.

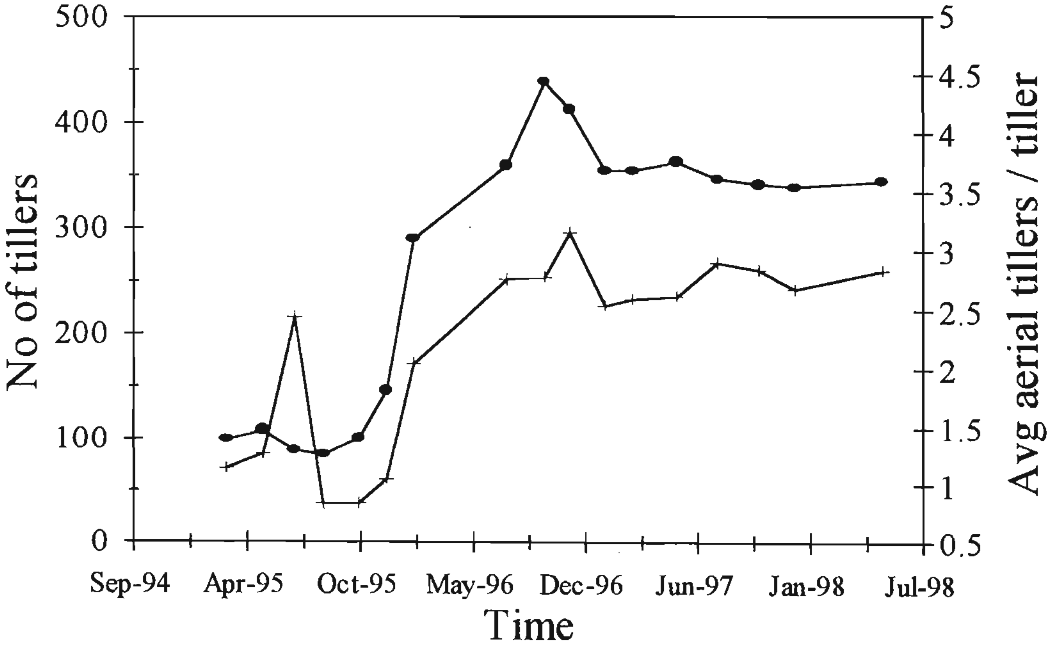


Figure 6.2 The number of rooted (●) and aerial tillers (+) in a population of tillers on the edge of a large *Stipagrostis amabilis* clump.

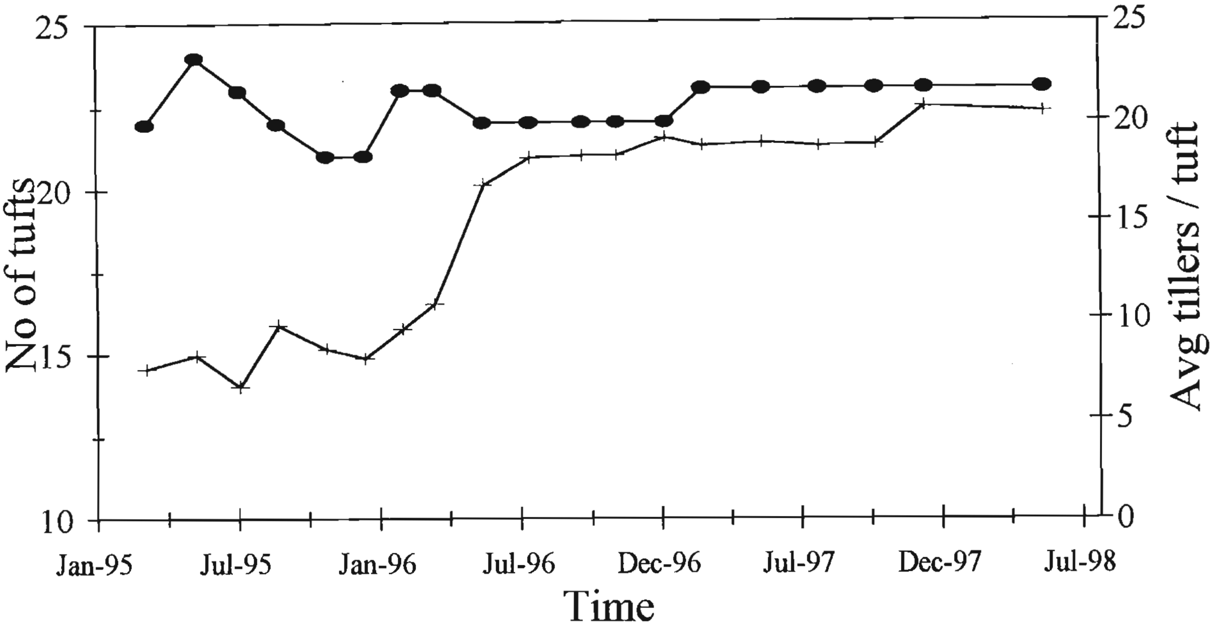


Figure 6.3 The number of small *Stipagrostis amabilis* tufts (●) in a demarcated area, and the average number of tillers per tuft (+).

four-fold in the example provided in Figure 6.2). The tillering front of some tufts covered up one meter of bare soil during the study period. Thereafter, from Jan 1997 until Jun 1998, tiller densities remained relatively constant. The average number of aerial tillers per tiller followed a similar pattern (Figure 6.2). Based on this information it is impossible to predict the future dynamics of these large clumps. Although it is possible that these large clumps will die back during the next dry period, its further expansion during the next very wet period remains to be tested. It is however clear that the observed tiller density can be sustained under normal rainfall conditions.

The density of relatively small *S. amabilis* tufts decreased slightly during the latter part of 1995, but remained relatively constant during the rest of the study (Figure 6.3). There was, however, a large increase in the number of tillers per tuft in reaction to the higher soil moisture levels following the Dec 1995 rainfall event, but thereafter the number of tillers per plant remained relatively stable.

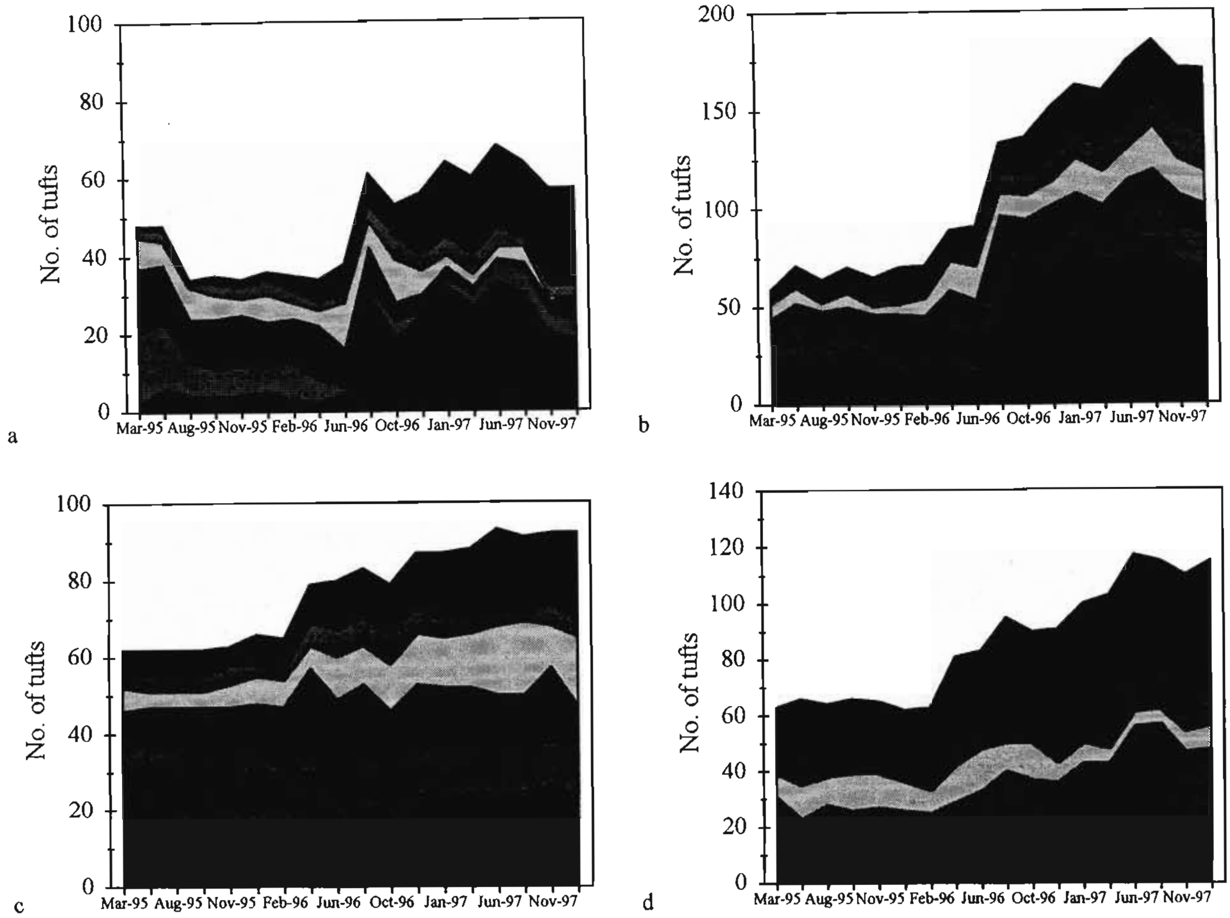


Figure 6.4 The total number of *Stipagrostis ciliata* tufts at each of the four sites studied (a – d are sites 1 to 4 respectively. The number of tufts in each size class is indicated; from the bottom to the top they are: 0 - 20, 21 - 40, 41 - 60, 61 - 80, 81 - 100, >100cm in circumference.

Stipagrostis ciliata

Results for the four *S. ciliata* populations monitored varied between very small increases in the density of tufts at site 1, to an almost logistic increase at site 2, with moderate increases at sites 3 and 4 (Figure 6.4).

The production of inflorescences, assumed to be an indication of seed production, was dependent on the size (circumference) of the tuft (Figure 6.5a). It is important to note that plants in the smallest size class (classified into the <11 cm circumference class) often produced inflorescences. Plants produced small numbers of inflorescences during the early part of the study, which was drier than the period after December 1995 (Chapter 4) when a far greater number of inflorescences were produced (Figure 6.5b).

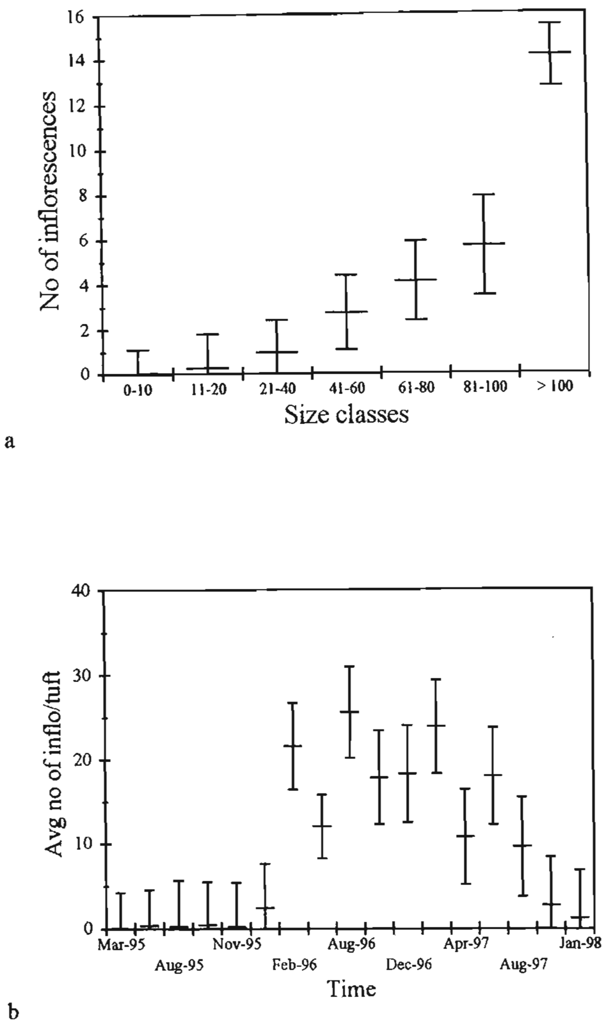


Figure 6.5 (a) The relationship between the number inflorescences produced during the entire study period and tuft size. (b) The average number of inflorescences produced at site 2 during the study period. Vertical bars indicate 95% confidence intervals

Seedling recruitment was opportunistic, and only occurred on a meaningful scale between the June 1996 and August 1996 sampling periods (Figure 6.6a-d). Effective cumulative recruitment (ECR) (i.e. cumulative seedling recruitment less death of seedlings recorded between sampling periods) was relatively low but stable during the dry period, which indicates at least some turn-over of seedlings during that time.

During the wet period of the study ECR was variable; at the first and second site it fluctuated (Figure 6.6a,b), but remained high, while at site 3 (Figure 6.6c), it may have reached an asymptote. ECR at site 4 continued to increase during the wet period of the study (Figure 6.6d).

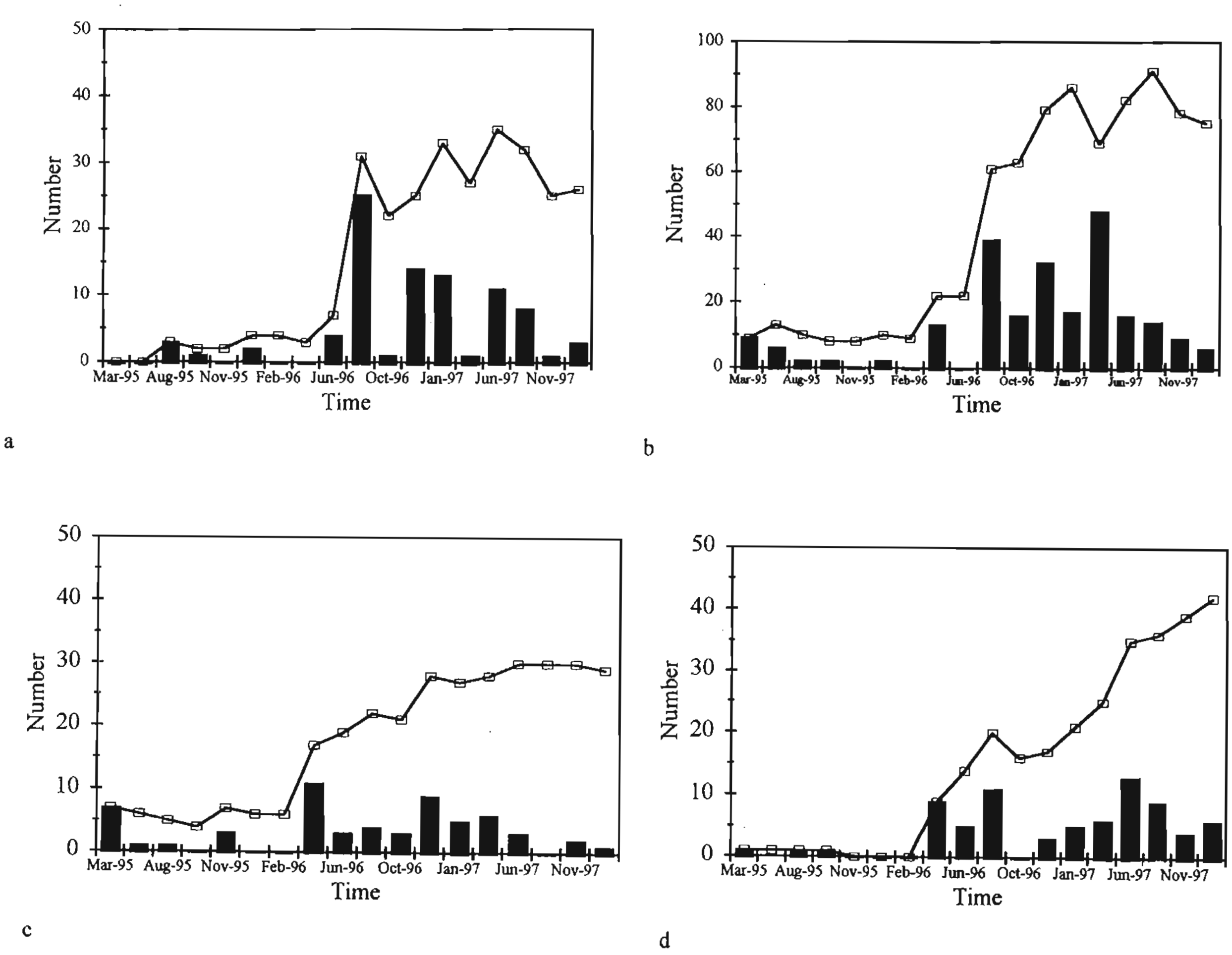
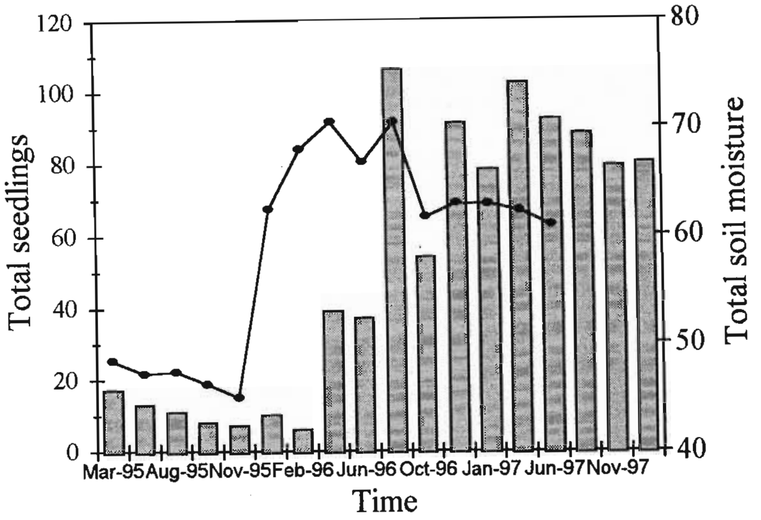
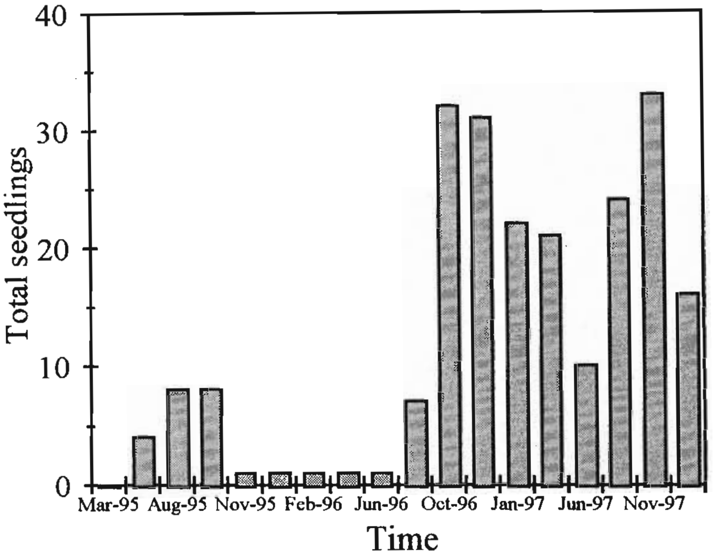


Figure 6.6 The number of new *Stipagrostis ciliata* seedlings counted during each sampling interval (bars), and the effective cumulative recruitment at each of the sites studied (□), a – d are sites 1 to 4 respectively.



a



b

Figure 6.7 (a) The sum of the *Stipagrostis ciliata* seedlings (bars) counted at the four sites, and the total soil moisture (●) at a nearby site devoid of any vegetation. (b) The sum of the *S. ciliata* seedlings that died during the sampling intervals, at the four sites studied.

There was a positive relationship between the total number of seedlings counted at all four sites and the soil moisture content measured at a nearby site devoid of any vegetation ($r=0.6$; $p < 0.05$, see also Figure 6.7a). Contrary, seedling death was not related to soil moisture, as measured at this scale (Figure 6.7b). Because more seedlings died during the wet part of the study, when there were many seedlings present, it can be said that seedling death is a function of seedling availability. This does not, however, exclude moisture stress as a possible cause of individual seedling mortality.

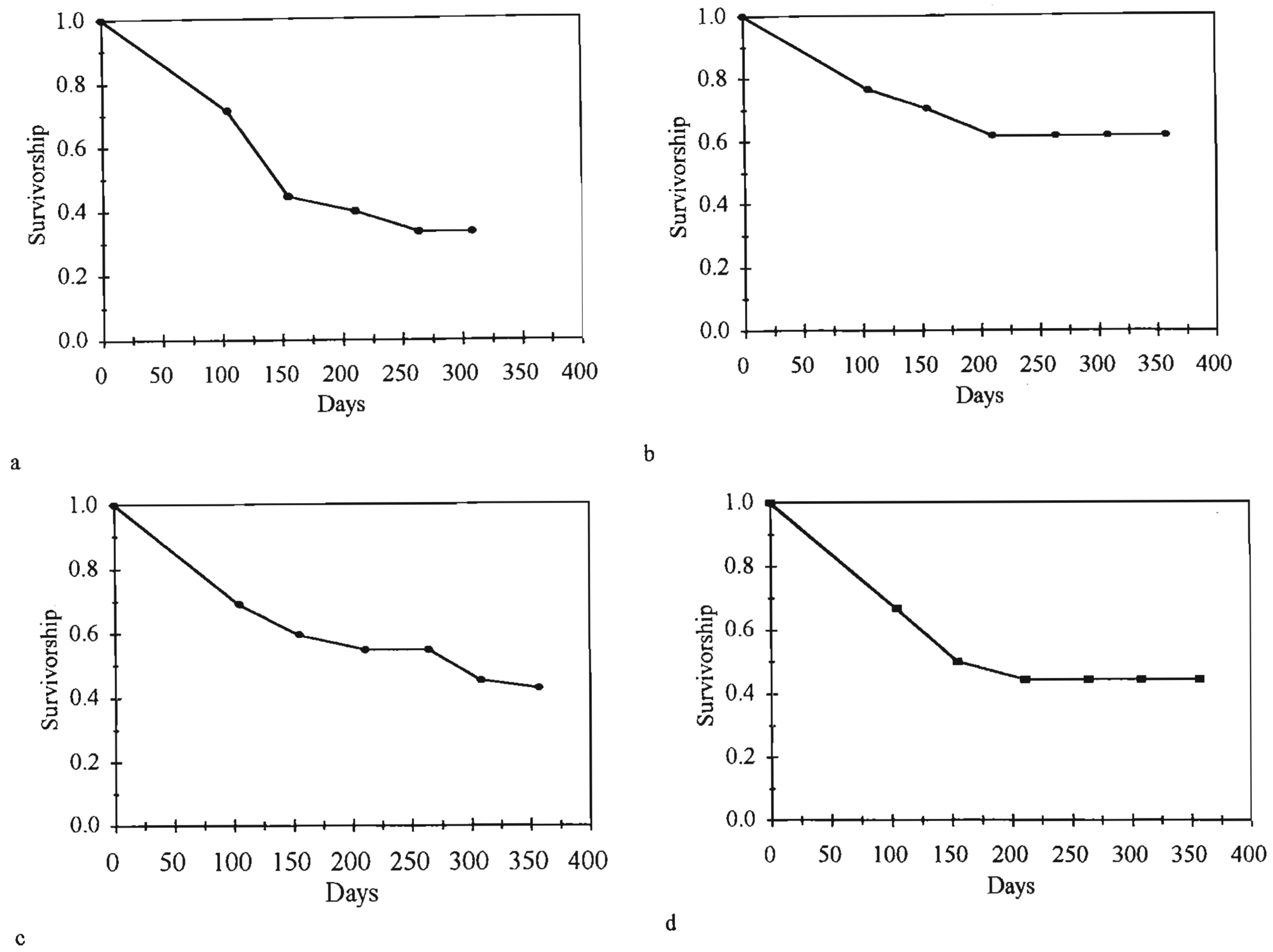


Figure 6.8 Survivorship curves of *Stipagrostis ciliata* seedlings at the four sites studied (a-d). The curves are based on all seedlings studied over the entire study period and do not therefore include the effect of season.

Sample sizes were insufficient to determine seasonal influences on seedling survivorship curves. Seedling survival to one year was lowest at site 1 (36%) and highest at site 2 where survival to one year was 62% (Figure 6.8a,b). The probability of seedling mortality is greatly reduced after 200 days. Most seedlings that passed this age, although then still relatively small (<15 cm circ.), survived for the rest of the study period.

Adult mortality was low and constant between most sampling periods of the year, apart from those which terminated in August, when significantly more deaths occurred ($F=2.16$, $p<0.05$) (Figure 6.9). Mortality of adult tufts was not different amongst size classes greater than 20 cm in circumference.

The proportion of dead tillers increased with tuft size (Figure 6.10a). Larger tufts may deplete the moisture or nutrient levels in their root zone quicker than do smaller plants, resulting in a larger proportion of dead or dying tillers. The proportion of dead tillers in all adult plants (>20cm circ.) increased during the dry (early) part of the study, and were markedly lower after the December 1995 rainfall (see Chapter 4), when sampled in January 1996 (Figure 6.10b). The proportion of dead tillers increased again towards the end of the study when rainfall was once again lower and population densities were higher. By far the largest proportion of tufts, in all size classes, were inundated with sand rather than eroded (Figure 6.11a). Although a small proportion of seedlings suffered from erosion, the data indicates that the majority was not affected by erosion nor by inundation. A large proportion of seedlings died, or simply disappeared (Figure 6.7b). Some of these deaths may be ascribed to erosion and inundation unnoticed by the observers because the seedlings are small and would, once eroded, blow away completely, or would not be detected if completely covered by sand. Larger tufts did not seem to suffer any consequences of inundation.

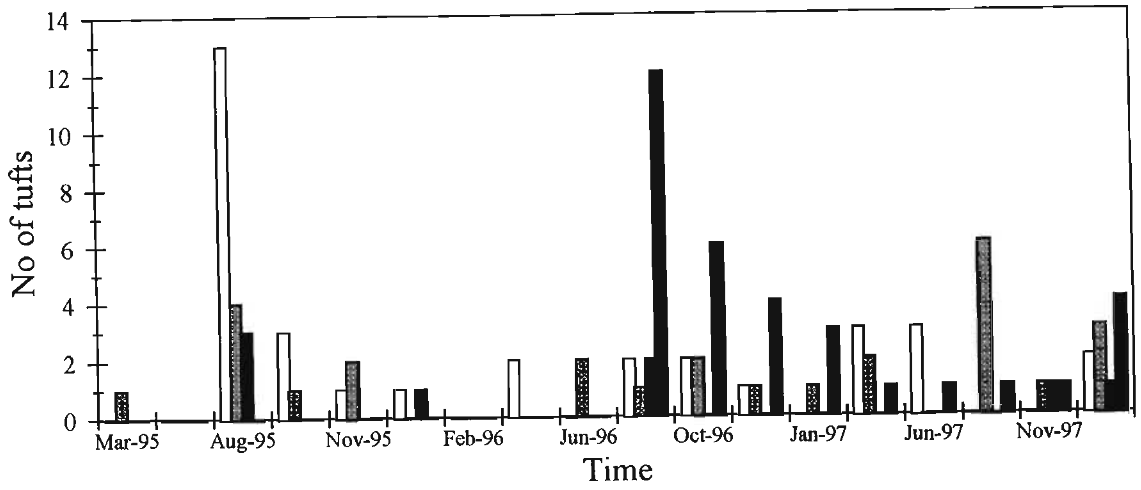


Figure 6.9 The number of adult *Stipagrostis ciliata* tufts which died during each sampling interval. Sites 1: white, 2: light grey, 3: darker grey and site 4: black.

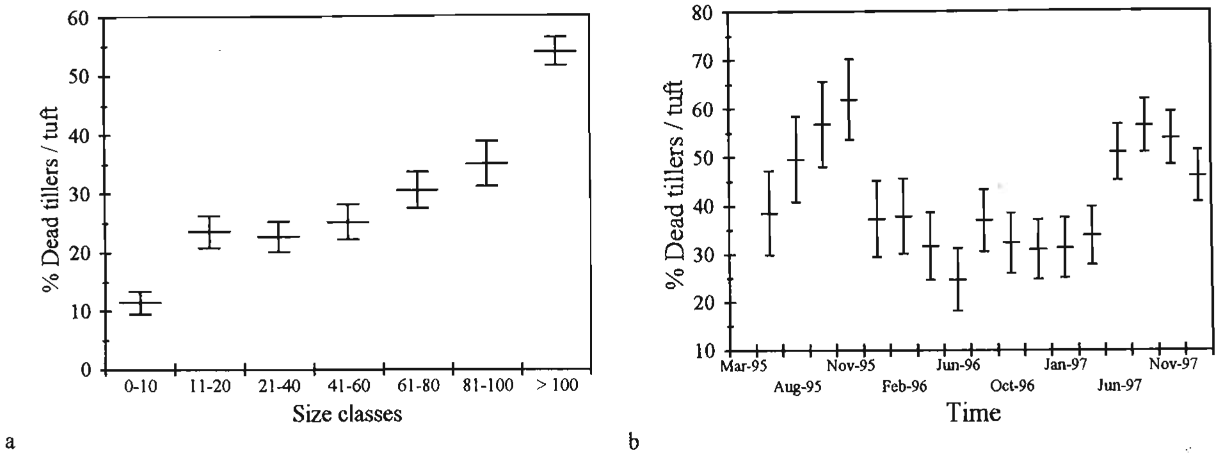


Figure 6.10 (a) The proportion of dead tillers within *S. ciliata* tufts in relation so to tuft size during the entire study period. (b) The proportion of dead tillers per tuft at site 2 during the study period.

Of all the plants that suffered from 'slight' and intermediate levels of erosion, more larger plants were eroded than smaller plants (Figure 6.11a). This is probably a result of greater wind speed around the base of larger tufts than around smaller tufts. The average erosion score decreased (thus more eroded) during the course of the study (Figure 6.11b). The cause of this is unclear, because intuitively one would expect reduced wind speed with greater plant cover. The direct opposite may, however, be the cause. Wind speeds over dunes with some vegetation may be higher closer to the

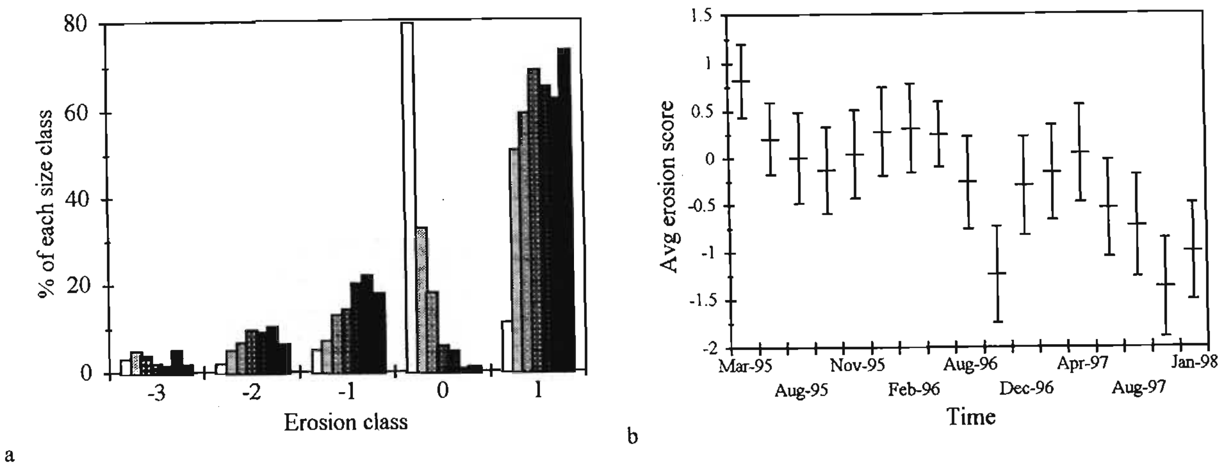


Figure 6.11 (a) The proportion of each *Stipagrostis ciliata* size class classified into the different erosion classes, -3: severely degraded to +1: inundation by sand. (b) The average erosion score at site 2 during the entire study period.

surface because the available space for wind to pass through a greater number of plants is less. Alternatively it may be because there are more, larger plants than smaller ones at the end of the study.

Damage to tufts by all herbivores was minimal. On only a few occasions were plants completely destroyed by herbivores, and in all these cases, the cape springhare *Pedetes capensis* was responsible. All the plants were inspected for evidence of grazing on all 17 sampling events and results were similar between sites. At site 2, this resulted in 2086 observations, of which there were 317 (15.2%) observations of fresh grazing, only 116 could be attributed to specific large mammalian herbivores, based on animal tracks. Springhare *P. capesis* were responsible for 46.7% of these grazing incidents, springbok *Antidorcas marsupialis* 43.9%, scrub hares *Lepus capensis* 8.6% and steenbok *Raphicerus campestris* 0.8% of the grazing incidents. No attempt was made to quantify the amount of vegetation removed. The proportion of tufts with fresh evidence of grazing increased with tuft size (Figure 6.12).

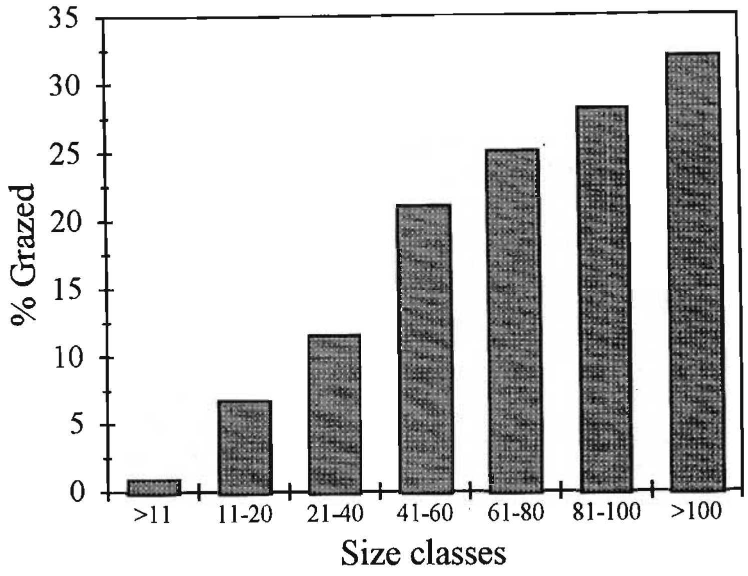


Figure 6.12 The proportion of *Stipagrostis ciliata* tufts grazed in relation to tuft size.

Together, the relatively low observed herbivore impact on adult tufts, the large number of seedlings that established and the relatively low rate of seedling morality result in increases, not only in the number of plants per unit area, but also in larger individual plants. Circumference and height of the 'adult' plants marked during the first sampling exercise increased significantly during the rest of the study period (Figure 6.13a&b). The observed increases in the number of tufts and the size of the tufts resulted in four- (site 2) to six-fold (site 1) increases in the basal cover of *S. ciliata* at each site (Figure 6.14).

This data illustrates that although recovery of *S. ciliata* populations may vary in terms of numbers, the combination of increased plant size and the increased number of plants result in a substantial increase in the total basal cover.

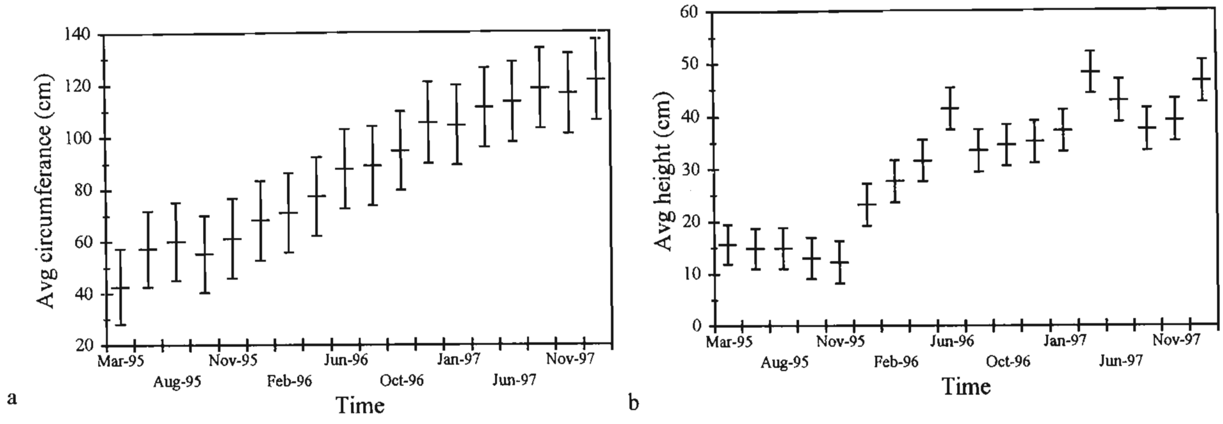


Figure 6.13 The growth in (a) circumference and (b) height of the *Stipagrostis ciliata* tufts which were present at the first sampling period.

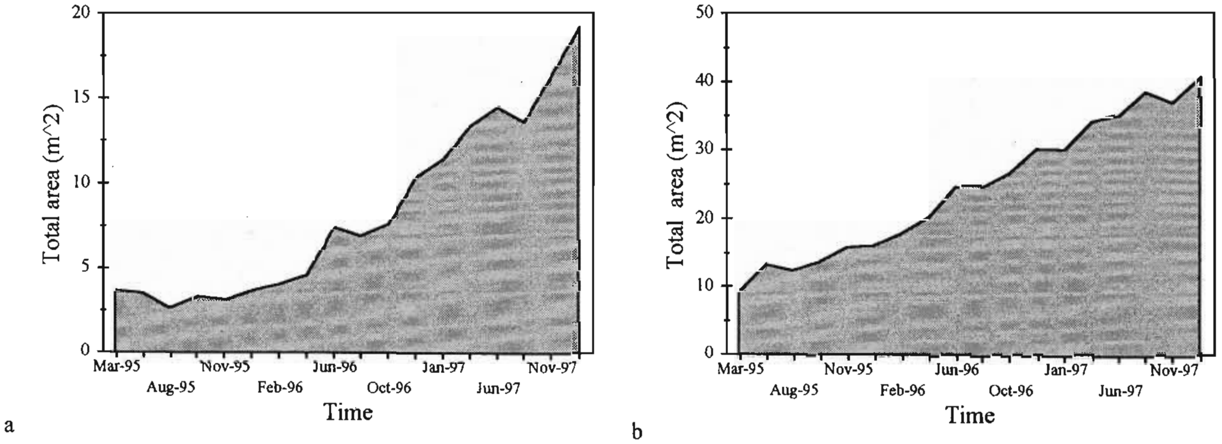


Figure 6.14 The total basal of *Stipagrostis ciliata* at (a) site 1 and (b) site 2 during the study period.

Discussion

Rainfall is considered as the primary driving force of vegetation dynamics in arid and semi-arid areas (Noy-Meir 1973). The number of *S. amabilis* tillers increased in reaction to a rainfall event following a relatively dry period, during which time tiller numbers were relatively stable. The increased tiller populations were, however, only maintained for two of the 'growth forms' studied. Where loose individual tillers occurred, their density at the end of the study was reduced to the same level as that at the end of the dry period. The other two 'growth forms' studied also increased markedly in reaction to the rainfall events of Dec 1995, but remained stable thereafter, when rainfall was close to the long-term annual average. These two growth forms of *S. amabilis* are thus able to maintain themselves during average rainfall years and can most probably react positively to periods of higher moisture availability. Although no such variations in rainfall occurred during the latter part of the study to confirm this, it is probable that the *S. amabilis* populations will be determined by the combination and sequence of dry and wet periods. There was no difference in tiller dynamics with regard to grazing. Even though the stocking rate during the study was very low, *S. amabilis* is not a very palatable species, but its role in stabilising dunes is of crucial ecological importance. The data suggests that recovery at low stocking rates, is possible, although very slow, at this spatial scale, and that it is promoted by high rainfall events.

The increases in the number and size of *S. ciliata* tufts, and consequently the increased total basal cover within the monitored areas, unequivocally indicates the recovery of *S. ciliata* populations at the patch scale. *Stipagrostis ciliata* is regarded as more palatable than *S. amabilis,* but the stocking rate at the study site seems to be conducive to the recovery of *S. ciliata* at this scale. The variation in size distribution between sites, and changes in size distribution within sites, over time (Figure 6.4) indicates some degree of variation in the dynamics of *S. ciliata.* As smaller plants grew into the largest size class, the proportion of large plants in Site 1 increased, but these smaller tufts were not 'replaced' by the growth of new seedlings. On the other hand, at site 4, where the largest size class also increased in number, the distribution of plants in the smaller classes remained relatively constant, indicating constant growth from one class to the next. The size of the plants first sampled increased consistently during the rest of the study period (Figure 6.13a), indicating that size is a good estimator of tuft age. It is thus reasonable to assume that the age distribution of the plants in site 1 was skewed to older and younger plants towards the end of the study.

Inflorescences are produced at any time of the year (Figure 6.5b) when moisture is available. Actual seed production and seed viability was not quantified during this study, but judging by the numbers of seedlings, seed availability at these sites was not a limiting factor. When soil moisture conditions were favourable, seeds germinated readily at any time of the year, including during the colder winter months (Figure 6.6a-d). Seedlings that germinate during the colder months may establish and develop a deeper root system that will place them at a competitive advantage to those seedlings, which only germinate in response to rainfall during the hot summer months. *Schmidtia kalahariensis* germinates in large numbers in response to summer rains in the degraded interdunes. The survival of *S. ciliata* seedlings amongst these *S. kalahariensis* seedlings is extremely low. In an opportunistic experiment, all the *S. kalahariensis* seedlings were removed in a plot where 98 *S. ciliata* seedlings had established. In another plot, 88 *S. ciliata* seedlings were left to contend with the competitive effect of the *S. kalahariensis* seedlings. Six months later, 65 (66%) and 2 (0.2%) *S. ciliata* seedlings survived in the cleared and uncleared plots respectively. This competitive effect of *S. kalahariensis* on *S. ciliata* may explain why interdune areas are still largely devoid of perennial grasses, while the dunes are colonised by *S. ciliata*, which in pristine conditions actually occurs in larger numbers on the lower slopes of the dunes and in the interdunes.

Tsoar (1990) stated that dunes are not ideal habitats for seedlings. Results here, however, indicate that once a seedling passed the age of approximately 200 days, mortality is greatly reduced. This may be also be related to the rate of root development through the dry soil layers near the surface to the depths where the soil is more or less constantly moist (Chapter 4, Figure 4.3). This requires further investigation.

With the low mortality rates of mature tufts (between 54 and 89% of mature tufts survived the entire study period of 38 months), a viable base population is maintained even through reasonably dry periods. Furthermore, seedling mortality was also relatively low, which more than adequately compensated for adult deaths. Young plants, in relatively bare patches, are capable of producing seed within the first year. This increases the rates at which bare sites can be colonised.

The cause of seedling deaths could not be directly determined, because seedlings disappear soon after death. It is most probably related to desiccation, scarring and inundation by sand as suggested by Tsoar (1990). Although adult mortality occurred at all times, mortality was statistically more prominent in the sampling periods culminating in August (Figure 6.7). This provides circumstantial support for these two causes of death, as June to August are normally very dry months and highest wind speeds were recorded during this time.

Grazing impact was understandably low, as the particular study area was very lightly stocked with indigenous game species. Although the amount of vegetation consumed by the different herbivores were not quantified, the high incidence of springhare grazing is once again indicative of our unrealistic strategy to manage these areas effectively by considering only the impact of large herbivores. Nevertheless, the impact of grazing on the population dynamics of *S. ciliata* in areas under commercial stock farming requires investigation.

Although erosion was not highlighted as a major cause for concern this may, however, be a biased conclusion in the case of seedlings. In addition, scarring of seedlings by sand particles, may also contribute to mortality. More frequent sampling should indicate this because most seedlings simply disappeared completely between sampling periods, making the identification of the cause of deaths impossible. Larger tufts suffer from greater levels of erosion, and may contribute to other causes of death such as desiccation, especially where roots are exposed to direct sunlight.

The results of this investigation indicate that although recovery on the dunes is possible at the patch scale, it is also dependent on the particular plant species. In the case of *S. amabilis*, even the growth form of a specific species may control the capacity to recover. The rate of recovery is determined by rainfall. The results, however, suggest two different population responses to rainfall. The recovery of *S. amabilis* may be restricted to high rainfall events, while *S. ciliata* seems to require a threshold soil moisture content after which it is able to increase unchecked during 'normal' rainfall years. *Stipagrostis amabilis* may require higher rainfall events to expand, because moisture levels near the tillering front of large tufts may be rapidly depleted which restricts further tillering. On the other hand, *S. ciliata* seeds germinating in open areas, away from the root zone of other tufts, establish without competition. O'Connor (1991) also found colonisation rates influenced by life history, with rhizomatous growth having very slow colonisation rates.

Chapter 3 suggested that recovery of degraded rangeland is highly unlikely within the time frame of the agriculturist. It is likely that the landscape-scale processes, which prevent landscape-scale recovery, do not operate at all or effectively, at the specific locations where the recovering patches occurred. If that is the case, then these small changes may ultimately accumulate to have landscape wide effects. Alternatively, drought or other adverse conditions, which may occur on a temporal scale beyond that which is covered by this study, may reset these relatively small populations. The question however remains as to whether these small-scale changes will accumulate and filter through the hierarchy to have a landscape-wide positive affect, and how long it would take.

Chapter 7

Predation of non-indigenous seeds in the southern Kalahari

Introduction

Seed banks have an important ecological and evolutionary role in vegetation dynamics because they function as a reservoir of genes (Kalisz 1991). Local extinctions during periods when adverse conditions (e.g. drought, fire or heavy grazing) eliminate the established population can be prevented by the presence of viable seed in the soil. Consequently the survival of a viable seed bank during such disturbances can have lasting effects on post-disturbance vegetation dynamics.

The size and composition of the seed bank is determined by seed production, immigration and emigration through dispersal, losses through decay, predation and unsuccessful germination (Van der Wall 1994). Granivory is thus an important factor that can ultimately affect plant community structure (Inouye *et al.* 1980, Davidson *et al.* 1985). The principal granivores in most ecosystems are birds, ants and rodents. The latter two play the most important role in desert environments (Davidson *et al.* 1985).

Studies on the recovery of degraded Kalahari rangeland have drawn attention to inertia of recovery owing to a lack of seed availability (Chapter 3). Various factors that affect the recovery of degraded Kalahari rangeland were studied elsewhere (Chapter 3). The focus of this study was to determine the potential role of seed predation on the seed bank of degraded rangeland. The specific objectives were (1) to determine which were the main granivores (insects, rodents or birds), (2) to determine the potential impact of granivores on the seed bank in relation to rangeland condition; and to determine whether there were differences in the size and composition of the seed bank. The role of seed size and nutritional value in the selection of seeds by ants was also investigated.

Materials and methods

Experiment 1: The potential of seed predation by birds, rodents and ants.

This experiment was conducted during March 1995 in severely degraded rangeland, i.e. the inter-dunes had a high cover of the annual grass *S. kalahariensis* and the dwarf shrub *R. trichotomum* and no herbaceous perennial vegetation, while the dunes had almost no herbaceous vegetation. Indigenous grass seeds at the time of the study were unavailable because of poor rainfall the previous season. Four commercially available seeds; Tef, *Eragrostis tef;* manna, *Setaria* spp., millet *Panicum miliaceum* and sorghum, *Sorghum* spp., were made available to birds, small mammals and ants following the methods of Kerley (1991). Thirty feeding stations were set up, fifteen in a interdune and fifteen on the adjacent dune crest. At these two locations, three rows of feeding stations, consisting of five stations per row, 10 metres apart, were set up. Each of the three rows allowed access to only one of the three groups of granivores. Petri dishes (10 cm diameter) containing seed for ants were set flush with the sand surface and covered with 5 mm wire mesh to prevent access by vertebrate granivores. Dishes with seeds for vertebrates were raised 3 cm above the sand surface, with the stilts being covered with an ant deterrent (Vermox). Dishes were opened and closed at dawn or dusk to allow diurnal or nocturnal granivores access to different stations. Each feeding station comprised of four seed dishes, each dish filled with 5 g of one of the four seed types used. Dishes were refilled when necessary, the remains were collected after 72 hours and the weight of the seeds removed was determined. Because of the vast difference in seed mass (Table 7.2) it was decided to provide equal masses of seeds rather than equal numbers of seeds. Data was tested for homogeneity and analysed using ANOVA.

Chemical analysis

Sorghum seed mass was determined by weighing individual seeds (n = 50) while the other seeds were weighed in 10 groups of 50 and the mean determined. The percentage *in vitro* organic matter digestibility (IVOMD), neutral - and acid detergent fibre (NDF and ADF), crude protein (CP), dry matter (DM) and organic matter was determined by the analytical laboratory of the Agricultural Research Council: Range and Forage Institute. Ether extract and energy of each seed type was determined by the ARC: Animal Nutrition and Animal Products Institute.

Experiment 2

The objective of this experiment was to determine the relative impact of seed predation by vertebrate granivores (birds and rodents) and invertebrate granivores (ants). Experimental procedure followed that of experiment 1, but with the following changes. Vertebrates were treated as a single taxa, these trays were thus not covered at night and results shown for vertebrates thus include predation rates by both birds and rodents. Only ten seed trays per taxa were used, and no trays were placed on the dunes. Two sites were used; the first was the degraded site used in experiment 1 and the second was in good condition rangeland. Here the dunes are stable, and the vegetation of the dunes and inter-dune areas consisted mainly of perennial grasses.

The size and composition of the seed bank

To determine the size of the seed bank, soil samples were collected at the end of the growing season (April 1996) from the interdunes of rangeland subjectively regarded as good, medium and degraded ($n = 30$ in each case) using a 12 cm diameter cylinder inserted to a depth of 5 cm. The good and degraded sites were the same sites where the other experiments were conducted. These samples were distributed over sterile sand in a glass house, watered and the number of seedlings that emerged was counted daily. All seedlings that survived long enough were identified to genus or species level, and then classified as annual or perennial.

All statistical analysis were done using analysis of variance and linear regression using Statgraphics 5.

Results

Experiment 1

No seed predation was observed on the dune crest, while only one species of ant (*Messor capensis*) was seen removing measurable quantities of seed from the feeding stations in the interdune.

The rate at which the different species of seed were removed differed (ANOVA, $F=6.17$, df 3,16; $p < 0.005$). The smallest seeds, tef, were removed at the greatest rate followed by the others in order of increasing mass (Figure 7.1a). There was therefore a negative correlation between removal rate and the logarithm of seed mass ($r = -0.96$; $p < 0.05$). Combining the removal rates of the four types of seeds, a total of 2.76 g seed were removed per hour from

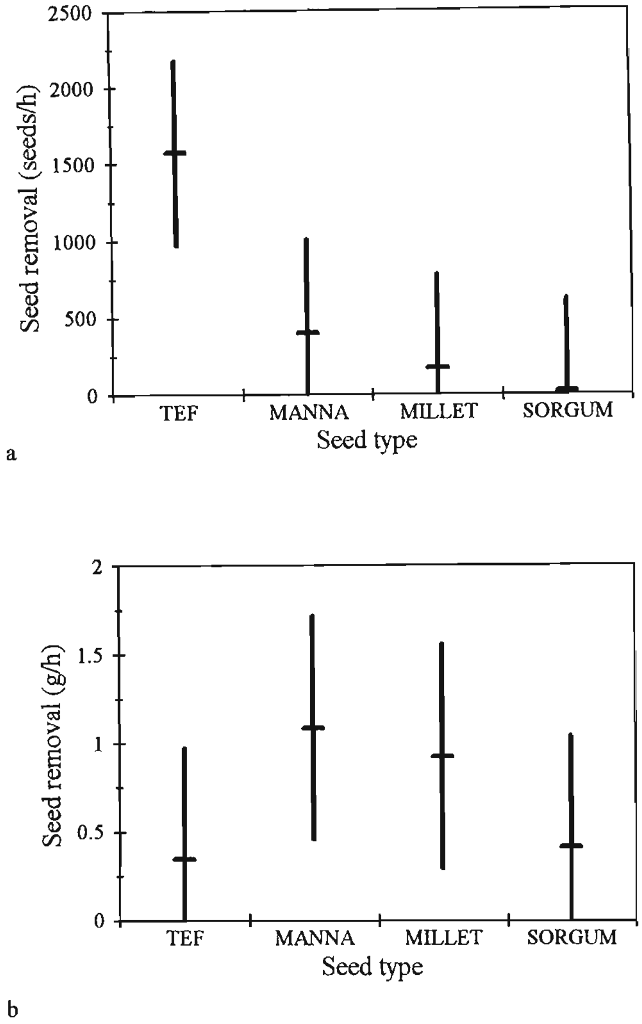


Figure 7.1 The (a) number and (b) mass of seeds removed from seed dishes by *Messor capensis* in degraded rangeland. Horizontal and vertical lines indicate the mean and 95% confidence intervals. $n = 5$ in all cases.

these dishes, which is equivalent to 2 163 seeds per hour. There was no significant difference between the mass of the different types of seeds removed per hour (Figure 7.1b), but the mean of tef does not lie within the confidence intervals of manna.

As an ant can carry only one seed at a time, the number of seeds removed is equal to the number of "ant trips" from the seed trays to the nest. Tef contributes in mass only 12.4 % of

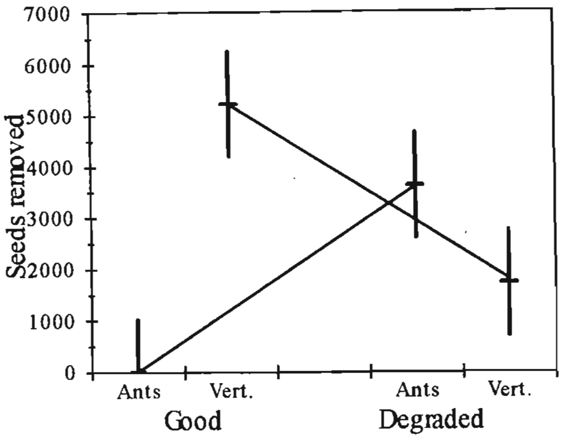


Figure 7.2 The number of seeds removed from seed dishes by ants *Messor capensis* and vertebrates (rodents and birds) in good condition and degraded rangeland. Horizontal and vertical bars indicate the mean and 95% confidence intervals respectively. $n = 10$ in all cases.

the seeds collected, however, most (72.6 %) of the "ant trips" were devoted to collect this seed type. Sorghum had a similar contribution (14.9 %) but only 0.8 % of the "ant trips" were devoted to the collection of this species. Manna and millet made up 39.3 and 33.4 % of the seed collected per hour, requiring only 18.6 and 8.1 % of the "ant trips" to do this. The observed and maximum (if all ant trips were devoted to a specific seed) energy gains were calculated (Table 7.1). There was no relationship between the number and type of seed collected and the observed energy gains.

Table 7.1 Mass of seeds used and the energy content per seed and unit weight. The observed seed removal rates per tray is given together with the realised energy gains and the estimated energy gain if all effort was spent on one species only

Seed	Seed mass (g±SD)	Energy g (kJg^{-1})	Energy Seed ($kJ\ seed^{-1}$)	Seeds taken $hour^{-1}$	Observed energy intake ($kJh^{-1}\ dish^{-1}$)	Maximising effort on a single species ($kJh^{-1}\ dish^{-1}$)
Tef	0.000219 ± 0.000006	16.95	0.00371	1569	5.83	8.03
Manna	0.0027 ± 0.000424	17.51	0.04728	401	18.99	102.26
Millet	0.0053 ± 0.00912	17.16	0.09095	175	15.92	196.73
Sorghum	0.0249 ± 0.0054	16.77	0.41757	17	7.03	903.26

Table 7.2 Nutritional attributes of seeds used in selection trials. All values are expressed as a percentage of total air dried mass. The last row indicates the relationship between the observed seed removal rates and the values in the column.

Seed	Mass	Dry matter	IVOMD[1]	Crude Protein	Ether extract	Organic matter	ADF[2]	NDF[3]	Cell contents
Tef	0.000219	93.25	88.87	10.78	2.15	97.80	10.27	24.82	75.18
Manna	0.0027	90.89	77.29	11.57	4.58	96.55	17.35	45.5954.3824.32	54.41
Millet	0.0053	90.71	87.86	11.39	3.91	96.44	13.01		45.62
Sorghum	0.0249	89.80	91.25	7.67	2.82	98.37	6.36		75.68
r with seeds h^{-1}	0.99 (p=0.013)	ns	ns	ns	ns	ns	ns	ns	ns

[1] IVOMD = *In vitro* organic matter digestibility, [2]ADF = Acid-detergent fibre, [3]NDF = Neutral-detergent fibre, Cell contents was determined as: 100 % - % NDF.

Table 7.3 The number of seedlings from good, medium and degraded rangeland which lived long enough after germination to be identified as annual or perennial, as well as the total number of seedlings observed.

	Good	Medium	Degraded
Annual	4	49	107
Perennial	14	5	2
Total	53	100	167

Chemical analysis

Of the chemical components of the four seed types tested (Table 7.2), only the percentage dry matter was correlated with the number of seeds removed per hour ($r = 0.99$; $p < 0.05$). Although the energy content per unit mass of seed did not vary greatly, energy content per seed did, with a strong correlation between seed mass and its energy content ($r = 0.99$; $p < 0.001$).

Experiment 2

Seed predation differed among taxa (Two-way ANOVA, F=10.84, $p<0.002$) but did not differ between rangeland condition classes (F=0.01, $p=0.9$) although there was a significant interaction between condition and taxa (F=50.2, $p<0.0001$, Figure 7.2). Further investigation (with the decomposed model) indicated that ants removed more seeds in degraded rangeland ($p<0.01$) than vertebrates and that vertebrates removed more seeds in good condition habitat than ants ($p<0.05$). Vertebrate seed predation in good condition rangeland was primarily by rodents, while birds were the important granivores than rodents in degraded rangeland. The vertebrate taxa responsible for removing seeds from the dishes could be identified by the tracks in the sand around the seeds trays.

The size and composition of the seed bank

The average number of seeds that germinated per soil sample collected from degraded rangeland differed significantly from samples collected in good and medium condition rangeland (F=27.17, $p<0.0001$) (Table 7.3). The proportion of annual species that germinated and survived long enough to be identified as either annual or perennial, increased from good condition to degraded rangeland. The proportion of perennial species showed the opposite trend but much fewer individuals were present (Table 7.3).

Discussion

No seed predation could be detected on the degraded dune crests. These dunes have very little vegetation cover and vertical sand movement is therefore considerable (chapter 3). Dune crests are consequently relatively seed free and the unstable surfaces render them unsuitable for ant nests. No *M. capensis* nests or individuals were ever seen on the degraded dune crests. Granivores foraging on degraded dunes crests are thus unlikely to be successful.

In the interdunes, however, *M. capensis* removed vast numbers of seeds from the seed dishes, and spent much more time collecting the smaller (tef) seeds. Seed selection of granivores depends on the physical, spatial and nutritional characteristics of the food resource (Crist and MacMahon 1992). Of the nutritional characteristics of the seeds investigated, only the dry matter content correlated well with seed removal rates (Table 7.2). In terms of energy return, more time should be spent collecting the larger seeds (Table 7.2). None of the factors investigated in this study (except percent dry matter) can explain the observed selection of seeds, there were thus most probably other factors not taken account of in this study that determined *M. capensis* preference for tef seeds. The seeds used in this study, apart from the tef seeds (which resembles that of *E. lehmanniana*), are foreign to the granivores of the Kalahari. Further investigation using indigenous seeds should be done.

During the first experiment, vertebrate granivores removed very few seeds from the seed dishes in the degraded rangeland. However, during the second experiment vertebrates (mostly birds, judged by the tracts in the sand) removed some 6000 seeds (during 72 hours), while rodents were responsible for the greatest seed predation in the good condition rangeland (Figure 7.2). Seed predation by ants in the good condition rangeland was insignificant.

There is thus a clear interaction between rangeland condition and seed predation rates by the different granivores. Seed predation by vertebrates, and rodents in particular, were more important in good condition rangeland. Good condition rangeland has fewer seeds (Table 7.3) than degraded areas, because the perennial grasses generally produce fewer seeds. Soil samples from degraded areas contained more seeds (predominantly from the annual, *S. kalahariensis*) than good condition rangeland, and the contribution of perennial grass seeds was very small (Table 7.3). The large number of seeds in degraded areas may favour ant populations, resulting in increased seed predation in degraded areas. Elsewhere, one of three ants species studied by Valone *et al.* (1994) showed a positive correlation with plant cover.

Although it is appreciated that the technique employed during this study to determine seed removal rates does not reflect real predation rates (see Brown *et al.* 1975, Anderson and Ashton 1985), the relative removal and selection of seeds remains important. Therefore, if the selective removal of the non-native seeds reflects predation of indigenous seeds in the southern Kalahari, then only a certain subset of seeds will be removed from the seed bank as was found by Kelrick *et al.* (1986) and Whitford (1978). This selective granivory may result in a change in the density of the preferred plant species or even the composition of the plant community (Inouye *et al.* 1980) especially in the degraded state when perennial grass seeds are scarce. The influence of seed predation by ants on the size and composition of the seed bank in degraded Kalahari rangeland is thus potentially significant, but further investigation using indigenous grass seeds is required.

With regard to the management of degraded southern Kalahari rangeland, reseeding degraded interdunes would most probably be ineffective because of high seed predation rates. As the results indicate a preference for smaller seeds, reseeding with relatively large seeds may be more successful, or smaller seeds may be seeded together with larger seeds to reduce predation pressure on the larger seeds. Other techniques such as the chemical treatment of seeds or by rendering the seeds unavailable to ants (Barrow and Havstad 1992) may also be considered.

Chapter 8

General discussion: Rangeland degradation in the southern Kalahari

Introduction

Stock farming is an important agricultural land use in the southern Kalahari throughout South Africa, Namibia and Botswana. Although the Kalahari is a sparsely populated area, a significant number of people are dependent on the natural resources provided by this arid landscape. The Mier area is no exception, and probably harbours the greatest density of people in the Kalahari, within the limits of South Africa. Livestock production, on an individual basis, and a very well organised communal game production system provide the greatest contribution to the economy of the area. The Mier community as well as the local and provincial government considers any factor which threatens this income in a serious light.

What is rangeland degradation in the southern Kalahari?

Rangeland degradation has been defined in many ways, but it was the consequences of rangeland degradation that forced the Mier community to consider this phenomenon seriously. Extreme cases of rangeland degradation in the southern Kalahari are visually prominent in the Mier area. Dunes become completely bare with mobile sand, while the interdune areas become invaded by the shrub *Rhigozum trichotomum.* Primary productivity on both these habitats in the degraded state is very low. However, it was not this initial unproductive state that concerned the people, but rather the inability of such rangeland to recover spontaneously once the degrading agents have been removed, even during higher rainfall years.

Local knowledge thus indicated that degraded Kalahari rangeland does not recover in a time scale relevant to the landowner. The aim of this study was to investigate the processes or factors that prevent recovery in the southern Kalahari, and to place into a temporal perspective.

Two quite different habitats, the dunes and the interdunes, make up the Kalahari dune fields. Although, the dunes and interdunes consist largely of sand, differences in the organic matter and associated nutrients (Buckley *et al.* 1987a, 1987b), fine material content (Lancaster 1986), and in the effect of wind on the stability of surface Lancaster 1985) renders the interdunes stable and relatively compact, while the dunes are less stable and consequently less compact. Furthermore, the finer texture of the interdunes result in slower infiltration and lower available moisture for plant growth relative to the coarser dunes (Tsoar 1990). The dunes can thus be considered as more mesic than the interdunes.

These factors result in two different plant communities on the dunes and the interdunes (van Rooyen *et al.* 1994), which also react differently to disturbances such as heavy grazing. Once the perennial grasses in the interdune areas are removed through grazing, the long-lived shrub, *R. trichotomum,* invades the interdunes (Moore 1989). The mechanism by which this happens is well described by the 'two-layer soil moisture model' (Walker and Noy-Meir 1982). Futhermore, Schlesinger *et al.* (1990) described a conceptual model of rangeland degradation in relation to the temporal and spatial distribution of soil resources. Their hypothesis suggests that grazing increases the heterogeneity of resources, which in turn facilitates the invasion of desert shrubs, which leads to further localisation of soil resources. Although this was not studied, it seems a plausible hypothesis for the interdunes of the southern Kalahari.

In certain areas, however, and most probably as a result of the absence of *R. trichotomum* propagules, perennial grasses are replaced by the annual grass *Schmidtia kalahariensis*. In cases where *R. trichotomum* was removed, chemically or mechanically after invasion, *S. kalahariensis* colonises the interdune areas. Thus, degraded interdunes in the southern Kalahari consist either of dense stands of *R. trichotomum* or *S. kalahariensis*. *Rhigozum trichotomum* productivity is low (Moore 1989) and *S. kalahariensis* produces organic acids (van Niekerk 1974) rendering the grass unpalatable when actively growing. Only once the grass has completed its lifecycle and the volatile acids have evaporated, can *S. kalahariensis* be consumed by ungulates, during which time it compares favourably with perennial grasses with regard to digestibility and crude protein content (van Niekerk 1974). Personal observations, substantiated by local knowledge suggest that these states, with their reduced productivity (*Rhigozum trichotomum*) or temporarily unavailable production (*S. kalahariensis*), seem to persist for times longer than the landowner can accept.

Degraded dunes are not (initially) invaded by woody vegetation, but become completely bare. This triggers a range of reactions that suggest that once a threshold, as suggested by Friedel (1991), has been reached, the system cannot revert or can even sustain itself to continue the degradation process, irrespective of the presence of any disturbance agent (Bradshaw 1987). The mechanism by which dunes are degraded can be summarised as follows: reduced vegetation cover, as a consequence of fire or grazing can no longer protect the dune's surface from the erosive forces of the wind. Once bare, or partially bare, sand movement on the dunes increases which, apart from eroding and scarring existing vegetation (Tsoar 1990), also results in the net loss of small soil particles from the dunes. As most nutrients are trapped in the finer soil particles (Gupta *et al.* 1981) these are lost, most probably to the adjacent interdune areas. Nutrient input on degrading dunes is reduced because less vegetation produces less litter and increased wind speeds on the dune surface remove most of the lighter litter material. This process results in dunes that are no longer crested but flat and smooth. In addition, there are no structures to trap seed and most seeds are blown over the dunes and into the adjacent interdunes. Seedlings that do emerge on the dune are most often eroded, inundated by sand or physically damaged by the saltating sand particles during windstorms (Tsoar 1990).

Vegetation dynamics on good condition dunes are controlled by soil moisture (Noy-Meir (1973) referred to rainfall as the *master input*) and available nutrients. In this state, soil moisture determines the duration of the growing season and available nutrients determine the growth rate during that period (Scholes 1990). Once in a degraded state, however, moisture availability is no longer a limiting factor. Moisture levels remain reasonably high in bare dunes because no transpiration takes place and evaporation is limited to the surface layer (Tsoar 1990). Seed and available nutrients proximately determine the dynamics of dune vegetation but are more directly controlled by the survival of the seedlings in the unstable substrate. The primary determinant of vegetation dynamics on degraded dunes is thus wind. This change in the driving force of the ecosystem, from rainfall to wind, has serious implications for the recovery of degraded dune systems.

Thus, once a threshold has been reached where the vegetation dynamics on a dune is controlled by wind rather than by rainfall, the dune can not recover.

The role of diversity

S. amabilis is not a particularly palatable species, and although it is often the last species to remain on a degrading dune, its complete loss can not be ascribed to grazing alone. In such a state there may be very little else for the herbivores to graze, but the process of erosion and physical scarring described above may lead to the final demise of this species on degraded dunes. This species is critically important in maintaining the dune's stability and structure and is the only grass species that is able to withstand the onslaught of the increased wind speed on the dune crest. With very long-lived tillers and vegetative propagation through rhizomatous roots, *S. amabilis* can maintain itself in a fairly hostile environment where no other perennial grasses grow in significant proportions. The presence of this one species with reasonable cover is therefore most probably the last threshold before a dune's total destruction. The loss of various other species may thus reduce a dune's primary productivity, but not necessarily its resilience (and structure). Large isolated clumps of *S. amabilis* can persist on otherwise degraded dunes, but in many cases these are continuously eroded and grazed (as there is nothing else available) and may require drastic reductions in large mammalian herbivore numbers and continuous favourable rainfall conditions before they could colonise significant areas. The demise (and recovery) of southern Kalahari dunes thus depends largely on only one plant species. This questions the role of biodiversity as the only determinant of functional systems. In agreement with O'Connor (1995), true functional redundancy may not exist, but numerous species' contributions to consumable productivity are negligible, while others such as *S. amabilis* does not contribute significantly to the palatable portion of available plant biomass, but fulfil a crucial role in ecosystem functionality. Moreover, other species such as *R. trichotomum* and *S. kalahariensis* contribute to the total species richness but may impair rangeland productivity and functionality (with regard to vegetation productivity).

Southern Kalahari rangeland species can be divided into the following broad functional groups:

FISP (Functionally important species) contributing to rangeland productivity

This group includes perennial species such as *Centropodia glauca, Stipagrostis ciliata, S. obtusa, Eragrostis lehmanniana* and others. These species contribute significantly to biomass production, but any single species or any combination in any ratio, can sustain agriculturally viable primary productivity in the interdunes. Any of these species or any combination of these species (except *S. obtusa*, which is found exclusively in the interdunes) on dunes where *S. amabilis* occurs can sustain agriculturally viable primary production.

FISP contributing to important aspects other than biomass production

Stipagrostis amabilis is important not as a forage plant but for stabilising dunes, while plants such as *Acanthosicyos naudinianus* and *Citrullus lanatus* contribute mainly as a source of water to herbivores. Micro-organisms such as micorrhizae are lost from degraded dunes and probably also impair natural recovery of the dunes (Allsopp & van Rooyen *unpubl.*). These species do not contribute to the palatable biomass produced in these rangelands, but their absence reduces the system's functionality and most probably its resilience.

FISP that reduce or prevent sustainable biomass production

These species may produce high biomass, but it is not necessarily palatable, always palatable or produces very little palatable material. *Schmidtia. kalahariensis* produces a high biomass of temporarily unpalatable fodder which is only available once the plant has dried and its acids have evaporated. Total edible material may be high but is highly reliant on appropriate rainfall and severe bottlenecks in fodder-flow may occur in drought years during which germination of annual grass seeds may not occur. *Schmidtia kalahariensis* also prevents the establishment of perennial grasses and thus the recovery of the system to a state of more predictable biomass production. *Rhigozum trichotomum* on the other hand produces high quality fodder, but only for a very limited time of the year. It also prevents the establishment of perennial grasses and can persist for a long time (Moore 1989). Both these species may prevent severe erosion and may maintain important soil processes, but are not desirable from an agricultural (or conservation) point of view.

Functionally unimportant species or species with unknown functionality

Various grass species, which occur in low densities, and a plethora of forbs and dwarf shrubs are seemingly unimportant in maintaining the ecosystem's functionality (and productivity), especially from a pure agricultural point of view. However, many of these species may for instance contribute to the diet of the many granivorous species in the area. Their loss from the system may alter the composition of the seed bank and therefore the composition of the granivore component, which may ultimately have implications elsewhere in the food web. The seed harvesting ant, *Messor capensis* is very common in degraded Kalahari rangeland, most probably as a result of the increased supply of *S. kalahariensis* seeds, while rodents dominate the granivore community in rangeland where perennial grasses dominate. Once changes in species composition occur at one level they may result in changes at another.

The loss of biodiversity is also scale dependent. Species richness per unit area decreased significantly during degradation, especially at the very small scale (1-5 m^2), while there were very few species which are completely lost from the system at the 1 km^2 to 10 km^2 scale, even in the worst cases of degradation. The only functionally important species found to be completely absent in degraded rangeland at this scale were *Acanthosicyos naudinianus* and *Citrullus lanatus*. The most significant influence of degradation (at the landscape scale) was the changes in the cover and relative composition of important species.

Even *S. amabilis* was present in the most degraded areas at this scale, albeit in small clumps, which were unable to fulfil its functional role. True functionality therefore also has a density (or population size) component. Similarly, *S. kalahariensis* and *R. trichotomum* at low densities do not impair the system's ability to produce palatable plant biomass. From an agricultural point of view, it is not the number of species that determines southern Kalahari rangeland productivity, but the density of functionally important species and the ratio of the palatable to non-palatable functionally important species.

The role of scale and its influence on the landowners objectives

The role of scale on biodiversity has already been touched on in the previous section.

No rangeland is completely homogenous. Patches with different productivity occur and in the Kalahari dune blowouts may occur on dunes in otherwise good condition. The transition between these bare unstable areas and surrounding vegetation is very discreet and may or may not be stable. In degrading rangeland these blowouts, or bare patches, often increase in size and coalesce to result in predominantly bare dunes with smaller patches of surviving vegetation. Similar 'degrading' patches occur in the form of piospheres around water points. Depending on size of the piosphere (which is probably dependent on its age and the type and number of animals that use it) and the proximity of neighbouring piospheres, these may also coalesce and ultimately result in large completely degraded areas. The net effect of these degraded piospheres depends largely on the scale of investigation. For the individual landowner the loss in biomass as a result of a 1 km radius piosphere may be real.

At the scale of the entire Mier area, and in relation to other forms of degradation (such as *R. trichotomum* invasion) these piospheres may be insignificant.

Similarly, the observed small-scale recovery of degraded dunes where the cover of *S. ciliata* increases logistically in small patches is insignificant in relation to the size of the total bare areas at the landscape scale. A logistic increase in cover, no matter at how small a scale, suggests recovery, but the time scale at which recovery was observed in this study was very limited (three years). Continued dry and or very windy conditions may reset the *S. ciliata* populations again to a few tufts. The observed rate of recovery may thus be slower (or more variable) when observed over a longer time frame, and is dependent on the sequence of favourable and unfavourable environmental conditions.

Landscape scale ecosystem processes (and local knowledge) suggest that recovery of degraded dunes and interdunes are highly improbable because of the change from a rainfall to a wind driven system on the dunes, and the presence of stable monospecific vegetation communities in the interdunes. Small-scale observations at the patch level (1-50m^2) indicate logistic recovery, at least on a small temporal scale. These observations are not necessarily contradictory as they look at the same system at two entirely different scales. It will depend on the objectives of the investigation (or landowner) at which level he/she will focus a monitoring programme. In short, a monitoring system focussed on the very small scale will indicate very small changes in system dynamics, but is highly dependent on the temporal scale. Investigations at the landscape scale are less affected by temporal variability, but are less useful as an early warning system.

Similar scale-specific implications should be considered when evaluating the effects of certain management strategies. Great care should also be taken when considering the appropriate time frame of the investigation. For instance changes in a management strategy will only be apparent on the landscape level after a relatively long time. Although changes may be readily evident on the small scale, such changes should be carefully interpreted in relation to short-term climatic variation and site specific differences.

Conclusions of this study and its implications for rangeland management in the southern Kalahari

This study illustrated clearly that apart from habitat differences related to the coarseness of the substrate, moisture, nutrients and substrate stability, the two habitats (dunes & interdunes) harbour different plant communities and that these communities react differently to impact. Furthermore, the state of degradation of dunes and related interdunes is not linked. Most often interdunes are degraded first, or are in relatively poorer condition than the dunes (Chapter 3). This could be ascribed to the relatively drier conditions in the interdunes and consequent greater susceptibility, the higher nutrient status of interdunes soils which could result in greater preference by herbivores for interdune species, or simply because the interdunes are more accessible, especially to the poorly adapted domestic stock.

This study illustrates that degraded dunes, like interdunes, are unlikely to recover spontaneously from a degraded state to one with higher productivity. This in itself, once publicised, should act as a warning to prevent degradation.

The factors and processes described in this study which prevents spontaneous recovery indicate the basic restoration principles to be applied. On the dunes, sand movement should be limited, nutrient levels increased and seeds introduced or prevented from blowing across dunes. In the interdunes, the negative effect of *R. trichotomum* should be addressed by either killing the shrubs or removing them physically.

The availability of soil moisture does not restrain natural recovery of degraded rangeland in the Kalahari, and should thus not be a limiting factor when implementing restoration technologies. Rainfall on degraded dunes is mainly required during germination and early establishment of seedlings.

Degradation of Kalahari rangeland does not only lead to reduced productivity and resilience, but also to changes at other levels of the ecosystem; such as changes in granivore communities, which may in itself curb recovery.

Landscape wide processes may contradict the results of small-scale investigations, but these are dependent on the spatial and temporal scale of investigation and should be interpreted with in this in mind.

Landscape wide effects of management (and policy) can be investigated using remotely sensed data (TM was used in this study). Results obtained in this study indicate that with sufficient ground data (and on-ground verification), vegetation cover can be modelled and the state and extent of degradation can be determined.

This investigation clearly illustrates that the spatial impact of domestic stock and indigenous herbivores is different, and suggests that the impact around water points can be minimised, if not avoided completely, where game ranching is the major form of land-use.

Chapter 9

An ecological basis for rangeland restoration.

Introduction

The need for the rehabilitation of degraded rangeland arose after the realisation that the 'natural recovery' of degraded rangeland (to former levels of productivity) is either very slow or does not take place at all.

Although most models conceptualising vegetation dynamics incorporate a good theoretical basis for the need to restore rangeland, rangeland restoration has developed as a 'technology' rather than a science (Call and Roundy 1991). This approach has lead to the need for a theoretical framework for rangeland restoration (Tongway 1990, Call and Roundy 1991). Burton *et al* (1988) called for a thorough understanding of the processes controlling the composition and maintenance of vegetation communities to improve on the success of revegetation efforts. This is comparable to the view of other authors who pointed out that an understanding of succession is essential to rangeland revegetation (Allen 1988; Redente and dePuit 1988; Call and Roundy 1991).

Allen (1988) recommended that rangeland restoration should aim to facilitate the recovery of the (normal) ecosystem processes that drive succession. The objective is thus to restore or recreate a functional ecosystem within which sufficient genetic material is present to maintain the system's integrity and productivity during natural environmental stochasticity. This notion corroborates the views above, but also suggests that the theoretical framework for rangeland rehabilitation be based on models of "natural" vegetation dynamics.

The aim of this chapter is to provide a theoretical framework for the implementation of practical restoration projects. The first objective is to provide a framework within which to establish whether intervention is indeed required and then to establish what actions are required to stimulate recovery.

On defining range degradation

Various definitions of range degradation and desertification exist and a clear unambiguous definition that fit all situations is clearly not available. Despite the criticisms raised by Behnke and Scoones (1993), Abel and Blaike's (1989) definition of rangeland degradation is the most appropriate, at least in the current African context.

"Range degradation is an effectively permanent decline in the rate at which land yields livestock products under a given system of management. 'Effectively' means that natural processes will not rehabilitate the land within a timescale relevant to humans, and that capital or labour invested in rehabilitation are not justified.... This definition excludes reversible vegetation changes even if those leads to temporary declines in secondary productivity. It includes irreversible changes in both soils and vegetation" (Abel and Blaike 1989).

It defines degradation by using secondary productivity (animal products) as an index of rangeland degradation and does not use indices based on biodiversity or vegetation composition (and cover) which are in many cases inappropriate indicators of range condition. By not using diversity or cover as indexes, it includes rangeland of which the productivity has permanently declined because of the invasion of long-lived woody species (which can not yield secondary products). Examples of this includes vast tracts of land in southern USA encroached by *Prosopis* spp. and parts of the Kalahari now covered by *Rhigozum trichotomum* and *Acacia mellifera.*

Secondly, this definition stresses the difference between reversible and irreversible changes in primary and secondary productivity. A rangeland is thus either degraded (i.e. irreversible changes in primary productivity and thus secondary productivity) or it is not, which implies that the rangeland can recover and former levels of secondary productivity can be attained.

The definition incorporates a timescale, 'relevant to humans' to place terms such as 'never recover' and 'permanently degraded' into a realistic context. This may be a subjective inclusion, but in the real world, nobody can afford to wait more than a few years or a decade at the most for natural recovery to take place.

Models describing vegetation change (and degradation)

Milton and Hoffman (1994) listed three types of models: directional, cyclic and stochastic models that conceptualise grazing induced vegetation change in arid and semi arid rangelands. The order (chronological) in which these models are listed, is one of increasing complexity. This is the result of the realisation of the earlier model's inability to conceptualise certain features of vegetation dynamics in the arid and semi-arid areas.

Directional or range succession models are predominantly based on the Clementsian concept of plant succession (Clements 1916). The assumptions on which the model is based, (that there is only one 'climax', changes induced by improper management can be reversed by the removal of the disturbance (grazers), and, that the pathway of vegetation change, during recovery, is simply the reverse of retrogression) may not be valid for most arid and semi-arid rangelands (Westoby *et al.* 1989). Adaptations to this basic model by Bosch and Gauch (1991) and Bosch and Kellner (1991) provided changes in soil chemistry and reduced infiltration rates as reasons for irreversible states, but this in essence contradicts the establishment and maintenance of unpalatable perennial species.

Cyclic models propose that the dynamics of populations are primarily determined by oscillations in abiotic factors such as rainfall seasonality and quantity (Hoffman and Cowling 1990; Hoffman *et al.* 1990) or to biotic factors such as facilitation and competition among plant species (McAuliffe 1988; Yeaton and Esler 1990). The basic premise of this model is that the effect of grazers on vegetation dynamics is less than that of rainfall variability and interactions among plant species.

Stochastic models include state-and-transition models (Westoby *et al.* 1989) which suggest that vegetation dynamics are influenced by both biotic (grazing and plant-plant interactions) as well as abiotic factors such as drought or fire. An important feature of this model is the concept of irreversible transitions between states. These occur either because new species inhibit rather than facilitate the establishment of the original suit of species or because physical conditions have changed. Its ability to accommodate multiple stable states, in a non-linear fashion, is highly appropriate for arid and semi-arid areas.

The development of the state-and-transition model, and its wide acceptance by arid and semi-arid rangeland scientists, is indicative of the difficulties of explaining arid zone dynamics with previous models. In the process, and subsequently various other analogies, concepts and models were developed to explain or illustrate irreversible vegetation changes. Lewontin

(1969) introduced the "domain of attraction" analogy, which depicts the community as a ball in a cup. The walls of these cups depict the range of environmental conditions under which that community retains enough stability to prevent a transition to the next domain. Krebs (1985) developed this model further to introduce various domains with 'cups of different depth', indicating differences in the intensity of influences required to bring about a change in the community.

Friedel (1991) introduced the concept of *thresholds* to rangeland dynamics, it is said to be a "boundary in space and time between two states and the initial shift across the boundary is not reversible on a practical time scale without substantial intervention by the range manager". This clearly contains certain aspects of the definition used by Abel and Blaike (1989). These two concepts are complementary, in the sense that if a cup has a very high wall (on at least one side) the wall is effectively a threshold almost impossible to cross within a reasonable time scale. Furthermore, these concepts are also compatible with the state-and-transition model: certain transitions can occur, (a cup with low walls), while others may be impossible (irreversible, i.e. a cup with very high walls).

The mere existence and the effort spent on the development of models that conceptualise irreversible transitions are illustrative of this phenomenon's widespread occurrence. As such there are ample examples of irreversible transitions to effectively degraded vegetation states. Laycock (1994) refer to many such states from sites across the world.

When is restoration required?

At this point it is clear that restoration is only an necessity once irreversible transitions has taken place. Bradshaw (1987) elegantly explained the potential outcome of what can happen to a degraded area once the disturbance has stopped or is removed and what one should aim at achieving during restoration. He proposed a system with two main components, ecosystem function (biomass and nutrient content) and ecosystem structure (species and complexity). Once the disturbance has ceased, degradation may continue, it may remain stable or it may recover at various rates. If we accept the concept of degradation as irreversible vegetation changes, then the rate of recovery would be slow (in excess of decades) and restoration can be contemplated. The relationship between functionality and structure is then determined by the objectives of the manager.

How do we know that relaxing the grazing pressure (or other disturbances) will not suffice?

Clements (1916) proposed the theory of succession and its causes. Five causes were listed: (1) disturbance opening a site, (2) migrations of propagules to the site, (3) establishment of species at this site, (4) interaction of the species (shaping the community), (5) alteration of the site by the organisms present. These are the basic preconditions under which succession can take place. However, Pickett *et al.* (1987) suggested the use of a hierarchical array of successional causes (Table 9.1). The highest level defines the general and universal conditions under which succession will occur. It can be regarded as the answers to the question: What causes succession? (1) The availability of open sites, (2) the differential availability of species and (3) the differential species performance. These are the first level of the hierarchy, or the general causes of succession. The contributing ecological processes of conditions pertaining to the first-level causes, constitute the second level of the hierarchy. The third level of the hierarchy is the specific defining factors, which are required to make accurate predictions about the course of succession at a particular site.

The hierarchy of successional causes are of particular importance to the development of a rangeland rehabilitation framework. It specifically addresses the causes of natural revegetation, and when turned around can explain why natural recovery does **not** take place. Secondly, it stimulates a structured thought process focussing attention on both biological and environmental factors involved. With this in mind, I suggest that a clear distinction should be made between these factors. Although the environmental aspects can not strictly be seen as a cause of succession, it can definitely prevent it. The development of this dimension should complement the model, because the interaction between the environment (habitat) and biological (species) characteristics can explain various community responses.

Keddy's concept of assembly and response rules:

Keddy (1992) argued for an ability to predict the future state of communities and proposed the concept of assembly and response rules as a step in this direction. The first objective of assembly rules is simply to predict the presence of a sub-set of species at a specific location from the total species pool of the region. The second objective is to predict the abundance of each species at that location.

Species presence or absence is predicted based on the suitability of the species to the specific environmental conditions. Information regarding the species and the environmental characteristics is thus essential. The environment thus serves as a "filter", and only species with suitable characteristics will be able to establish and persist at the particular site. Two data sets are thus required, the total species pool, and a matrix giving the traits of the species in this pool. The information regarding the species traits could include data of a morphological, physiological or ecological nature. Furthermore, it should be stressed that this environmental filtering process acts on all stages of the plant's life cycle, and should be incorporated in the

Table 9.1 The hierarchy of successional causes. (From Pickett *et al.* 1987)

General Causes of succession	Contributing Processes or Conditions	Defining factors
Site availability	Coarse-scale disturbance	Size, Severity, Time, Dispersion
Differential species availability	Dispersal Propagule pool	Landscape configuration, Dispersal agents, Time since disturbance, Land use
Differential species performance	Resource availability	Soil conditions, Topography, Microclimate, Site history
	Ecophysiology	Germination requirements, Assimilation rates, Growth rates
	Life history strategy	Population differentiation, Allocation pattern, Reproductive timing
	Stochastic environmental stress	Reproductive mode, Climate cycles, Site history
	Competition	Prior occupants, Presence of competitors, Identity of competitors, Within-community disturbance, Predators and herbivores
	Allelopathy	Resource base, Soil characteristics, Microbes
	Herbivory, disease and predation	Neighbouring plants, Climate cycles, Consumer cycles, Plant vigour, Plant defence, Community composition, Patchiness

species' trait matrix. It is at this level that we find the connection with the first model. Pickett *et al.*'s (1987) third level of successional causes, the defining factors can be said to be analogous to Keddy's "environmental filter". This similarity will be illustrated in the next section.

Keddy's response rules follow logically out of the assembly rules. The next consideration after the initial establishment is: how will the species present respond to a change in one or more of the environmental factors? Two "steps" are required to predict the community after the environmental change: (1) the reaction of the existing species, which is the elimination of the species that does not "fit" the new environmental conditions (i.e. deletion rules) (2) the reassessment of the total species pool and the new environmental conditions, the inclusion of new species that can now establish and survive in the altered environment (i.e. addition rules). This is related to the concepts of facilitation and inhibition (Connel and Slatyer 1977). Once plants have established they can alter certain physical characteristics of the environment (habitat) that will "filter-out" certain species and allow other species to establish.

This rule-based procedure has important considerations for rehabilitation theory as it emphasises the importance of (1) an in-depth knowledge of the available species and the environmental conditions that persist in the degraded rangeland and (2) establishing functional communities that are able to respond in an natural way to environmental changes.

Applying the framework to rangeland rehabilitation in the Kalahari

Using the hierarchy of successional causes proposed by Pickett *et al.* (1987), I suggest a structured analysis of the system in question in terms of the general causes of succession (see Table 9.2). This would indicate at which level and what needs to be done in practical terms to initiate the remedial process (see Table 9.3).

As an example I will use data from this study, where heavy grazing has lead to large areas being extensively degraded to bare dunes and stable stands of annual grasses and shrubs in the interdunes.

From the *analysis of the contributing processes of conditions* in Table 9.2, it is clear that although sites are available for colonisation on the dunes (Chapter 3), the natural recovery of degraded rangeland is prevented by species availability (Chapter 7) and species performance. No colonisation of perennial grasses can take place in the interdune areas, because open sites are not available and, the few species (annual grasses and long-lived shrubs) that are present, perform so well that no other productive species (with regard to animal production) can establish (Chapter 3 – high density of *S. kalahariensis*). Species availability is also limited.

The required *managerial actions* outlined in Table 9.3 clearly indicate what is required to induce succession on the dunes and in the interdunes. Sites are available on the dunes, but species availability and species performance are limited. Species performance can be enhanced by species additions, but only limited success can be expected as only a limited number of species are available from the regional gene pool. The only option is thus to manipulate the habitat in such a manner that species performance would improve. Open sites for colonisation are not available in the interdune areas and species availability is limited. Those species present perform well, but introduced species may suffer from interspecific interactions as explained in the table. To induce the required autogenic remediation process would thus require the opening of sites, the introduction of suitable species and some manipulation to reduce negative species interactions.

Table 9.2 Potential primary causes of succession on degraded Kalahari dunes and interdunes and second level causes of success or failure.

General causes of succession	Analysis of contributing processes or conditions	
	Dunes	Inter-dunes
Site availability	Yes, almost denuded dunes	No, inter-dunes invaded by *R. trichotomum and S. kalahariensis*
Species availability	Plant diversity greatly reduced, very few species persist in localised areas	Two species dominate the habitat, other species are not present, not even in the seed bank
Species performance: Existing species:	The existing species are well adapted to undisturbed habitat, but environmental stress prevents colonisation	Existing species perform very well, most probably as a result of improved nutrient status
Species performance: Other species from the total regional genepool:	The success of other species under the current condition is likely to be limited, for the same reasons that the existing species perform poorly.	Although the existing species perform very well it is hypothesised that other species will not perform well because of interspecific interactions such as competition, possible allelopathy and different life history strategies.
Environmental characteristics	Increased moisture Reduced nutrients and mycorrhizae Increased sand movement	Reduced moisture Increased nutrients

Table 9.3 Developing rehabilitation procedures based on the constraints of succession listed in Table 2.

Causes of succession	"Action" with regard to the contributing processes or conditions	
	Dunes	Inter-dunes
Site availability	Open sites are available: no action	Sites are not available: Create open sites if it is a viable option.
Species availability	Some species are available but other suitable species should be introduced.	More suitable species should be introduced.
Species performance: Existing species:	Nothing further than the introduction of species better adapted to the specific condition, can be done.	Existing species perform very well, most probably as a result of improved nutrient status
Other species from the total regional genepool:	Other species should be selected (screened) from the total regional gene pool. Screening criteria should include the ability to cope with sand movement especially during the seedling stage.	Other species should be selected (screened) from the total regional gene pool. Screening criteria should include the ability to germinate early, grow fast and compete for moisture.
Environmental Characteristics	Increase nutrients and mycorrhizae Reduce sand movement	Increase available moisture

Practical rehabilitation techniques

The information assembled in Tables 9.2 and 9.3 was used to develop restoration techniques to be employed in the study area.

Dunes

Site availability

Degraded dunes are almost completely bare. Site availability as such is therefore not a problem.

Species availability and performance

Screen species for the following characteristics (based on measured environmental conditions):

(1) rapid germination and radicle development (in order to germinate quickly and enter the deeper, wetter levels of the dunes (see chapter 4);

(2) an ability to grow in low nutrient soil (see chapter 3);

(3) an ability to survive in mobile soils (see chapter 3);

(4) the ability to survive inundation during the seedling stage is important;

(5) the ability to cover rapidly large areas to stabilise sand.

Environmental Characteristics

Three significant changes take place with regard to the habitat during rangeland degradation: Reduced vegetation cover results in (i) increased soil moisture content (chapter 4) and (ii) increased sand movement (chapter 3) which are both very important limiting factors. As a consequence of this, (iii) nutrients are lost from the dunes (chapter 3). The degraded dunes need to be stabilized and the nutrient levels improved (Figure 9.1). In practice, *R.*

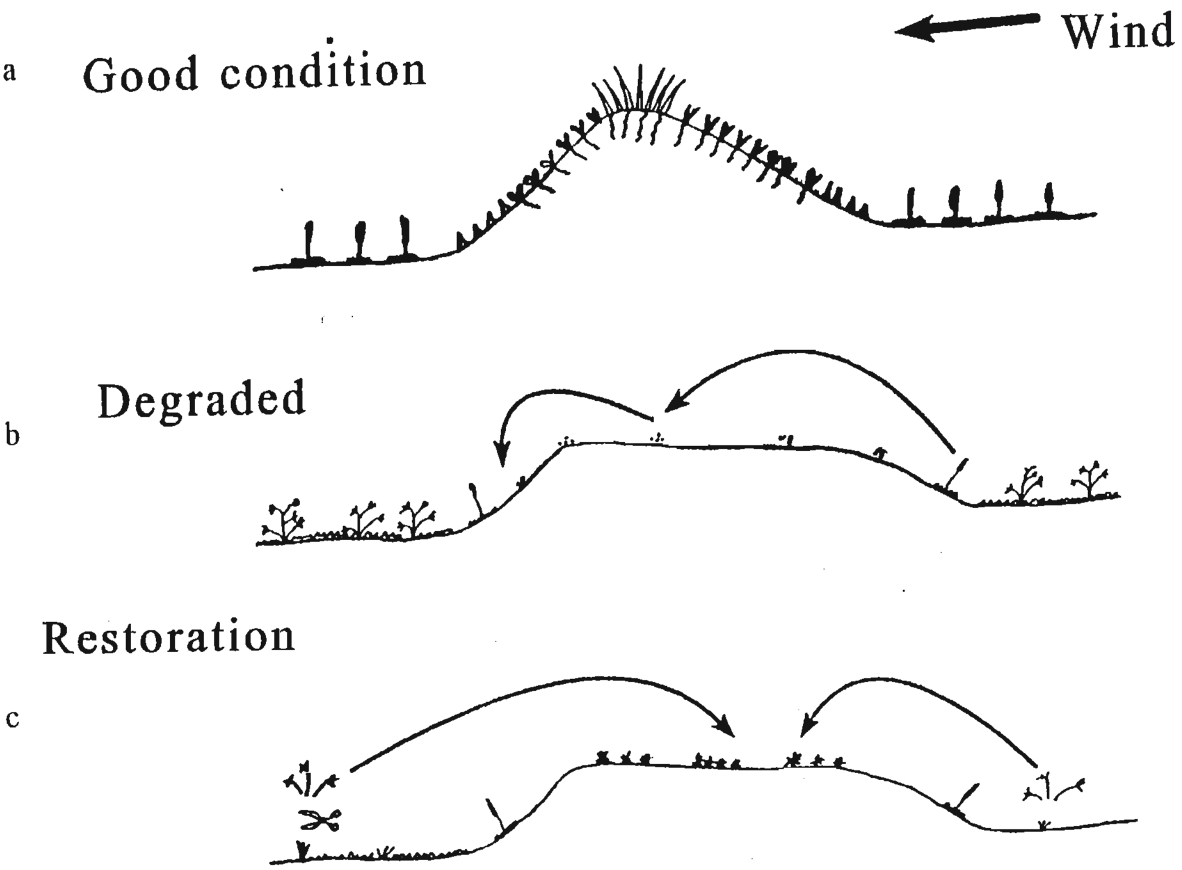


Figure 9.1 (a) Good condition rangeland in the southern Kalahari comprised of stable dunes with perennial grasses in the interdune areas. (b) Rangeland degradation results in loss of vegetation on the dunes, the dune structure changes and excessive sand movement and low nutrient availability prevents establishment of seedlings. The interdunes are invaded by woody shrubs and annual grasses. (c) The procedures applied to this system in order to initiate a remedial process.

trichotomum which increase in the interdunes areas during degradation are used to stabilize the dunes. Wind does not affect the surface of good condition dunes, because the vegetation protects it. Similarly, the packing of brush protects the sand and reduces the wind speed, close to the surface which results the deposition of suspended particles. These small particles with their relatively high nutrient content (chapter 3) enrich the otherwise infertile sand. In addition the brush also trap seeds that would have blown over the smooth surface of untreated degraded dunes. Preliminary results indicate that nutrient levels increase within a few months (van Rooyen and Brown unpubl). Although the same study illustrated the effectiveness of these barriers in trapping seeds, it was found that the perennial grasses do not germinate in the brush packs, but between and on the edges of the packed areas (van Rooyen unpubl data).

Interdune areas

Site availability

Dense stands of *R. trichotomum* prevent succession and open sites need to be created. This can be achieved by mechanical or chemical treatment.

Species availability and performance

Species that have the ability to establish amongst competitors such as *R. trichotomum* and *S. kalahariensis* should be introduced.

Screening criteria to select such species would include a very fast and a high rate of germination. They must be able to compete effectively for water and other nutrients while not being influenced by the potential allelopathic affects of *S. kalahariensis*.

Experience in the field proved that the removal of *R. trichotomum* results in monospecific stands of *S. kalahariensis*. Unless procedures can be devised to reduce these annuals, species with similar characteristics as described above need to be selected. Recent incidental observations indicate that certain perennial grasses (*Stipagrostis ciliata*) can germinate during the cold season during un-seasonal rainfall events. The phenomenon needs further investigation and may be used to give perennial grasses a temporal advantage over the warm season germinating *S. kalahariensis*.

Environmental characteristics

The interdune areas need no managerial intervention at the environmental level, unless drastic measures (such as ploughing) are required to establish small pockets of perennial plants from where seeds can disperse.

Conclusions

Using a structured process for the evaluation of degraded areas to determine what biotic and abiotic factors prevent succession, will provide the appropriate information to develop restoration procedures which focus on the factors limiting recovery. Such a strategy will thus eliminate the need for cost intensive 'shotgun' approaches.

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