Effects of frequent burning on grass-grazer interactions in a mesic savanna

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Abstract

Fires are often used as a management tool in both game reserves and rangelands to manipulate food availability for grazing animals. After fires, large areas of the landscape are quickly covered with nutritious new regrowth, which grazers move into and utilise as a food resource. The effect of this change in animal grazing patterns on the grass communities is not yet well understood.

Certain grass communities depend on heavy, continuous grazing for their persistence: they are out-competed by taller-growing species in the absence of grazing. Conversely, the taller-growing species die out under heavy grazing. Thus, in many savanna and grassland ecosystems, the grass community present in an area depends on how frequently and how intensively the area is grazed. Every year, fires in these systems are altering the distribution of grazing in space and time, by altering the proportions and distributions of short, palatable grass.

In my MSc I present data describing how fire alters grazing patterns, and I show how this can result in the disappearance of intensively grazed patches in the landscape. I also use a model to illustrate how this effect might be mediated by rainfall and grazer density, and by different fire regimes. I investigate long-term consequences of this process on the distributions of alternative grassland states in Hluhluwe Umfolozi Park and show that lawn-grass-dominated areas are associated with a less-frequent fire regime.

Thus, although large fires provide high-quality grazing in the short term, in the long term they could be limiting the amount of grazing in an area, because they prevent the initiation and spread of grazing-tolerant lawn-grasslands, which can support high grazer numbers and a high diversity of grazers.

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Chapter 1: Introduction

Fire and grazing are important modifiers of ecosystems, especially in savannas, where these two agents are often acting together. Independently, fire and grazing have been shown to influence vegetation composition, ANPP, water use efficiency, and nutrient cycling (*Grazing*: McNaughton 1985; Milchunas & Lauenroth 1993; O'Connor 1994; Hobbs 1996; Knapp *et al.* 1998; *Fire*: Tainton & Mentis 1984; Knapp *et al.* 1998; van de Vijver 1999; Russell-Smith *et al.* 2002).

More recently, considerations of the landscape/spatial effect of fire and grazing have also been investigated. Briggs *et al.* (1998) demonstrate how grazing increases spatial heterogeneity in tall-grass prairie. Adler *et al.* (2001) discuss how grazer foraging patterns create and respond to heterogeneity in the landscape. Although they are looking at browsing, not grazing, Pastor *et al.* (1988)and Pastor *et al.* (1998) show how moose browsing can influence patch dynamics and forest structure. Fire research has progressed from investigating the effects of fire intensity, season, and frequency to looking at spatial aspects such as fire size and patch dynamics. Clarke *et al.* (2002) and Brockett (2001) consider how spatial variability in fire regimes can influence patch mosaics, and the range of vegetation types represented in a landscape. Turner *et al.* (1997) looked at how fire size and pattern influence successional processes in Yellowstone National Park. Allan & Southgate (2002) state that large fires are affecting plant and animal diversity in spinifex grasslands in Australia.

These more spatially-oriented studies have been prompted by the recognition of the importance of understanding and maintaining heterogeneity in landscapes, and of the effect that vegetation structure and patch characteristics have on fauna and flora (Weins *et al.* 1993; Pickett & Rogers 1997).

However, fire and grazing have usually been investigated independently. There is very little research on the interaction between these two ecosystem control agents. Hobbs *et al.* (1991) showed that the effects of fire on nitrogen budgets in a grassland system were modified by grazing, but most grazing trials and experiments have consciously tried to exclude fire as a factor – in a recent review by Milchunas & Lauenroth (1993), of 276 grazing studies, there was no mention of fire. In Belsky (1986), the one reference that I did find, fire was included due to an accidental fire through the experimental site.

This research-gap is understandable when one considers that the scale at which fire and grazing interact is generally much larger than the plot-based scale at which the effect of fire and grazers on ecosystems has been studied: fire affects grazing by altering large-scale foraging patterns, and grazers affect fire by reducing fuel loads and altering fire spread in a landscape. Traditional experimental designs are not able to investigate how processes such as these affect ecosystem functioning.

However, landscape-ecological approaches are offering useful insights in many ecological disciplines (Lima & Zollner 1996; Bissonette 1997; Haddad 1999). The tools and techniques for asking ecological questions at landscape scales are constantly being improved (Turner 1991), and fire and grazing research are now at a level where spatial processes can be considered. I believed it was possible to test whether these two top-down control agents – fire and grazing – were interacting to affect grass communities.

Effects of fire on mammal grazing: an hypothesis:

In Africa, where indigenous mammalian herbivores are still an important part of natural ecosystems, grazing-lawn grass communities are recognised components of many landscapes. This term, coined by McNaughton (1984), is used to refer to areas "created and maintained by heavy grazing with unique assemblages of grazing-adapted grass species". *Lawn grass* species, which are typically short-statured and stoloniferous, are very different from taller, less grazing-tolerant *bunch grass* species, which have a caespitose growth form.

Extensive grazing lawns are found in the Serengeti ecosystem in East Africa, but their role in Southern African grazing systems has been largely unrecognised. Grazing-lawns, and the stoloniferous grasses associated with them, are not included in a recent review of grassland ecology (O'Connor & Bredenkamp 1997), and they have often been viewed by rangeland scientists as signs of degradation and poor management (Tainton 1999). However, in game reserves, much of the biomass and diversity of grazers is concentrated on these grazing lawns (McNaughton 1985; Owen-Smith 1988; Novellie 1989).

Because grazing-lawns are created and maintained by grazing animals, their extent and distribution in a landscape are likely to be influenced by the foraging patterns of grazers. It is in this context that I predicted that fire might be interacting with grazing to influence grass communities.

In the absence of fire, localised areas of intensive grazing develop frequently in a tall-grass landscape because of the positive feedback between grazing and palatability: previously grazed areas often tend to get re-grazed and kept short and grazing patches can develop (Hobbs *et al.* 1991; Laca 2000; Adler *et al.* 2001). The persistence of these grazed patches depends on their continued attractiveness to grazers. It has often been shown that fires affect grazers – attracting animals into burnt areas where the regrowth after fires is short, palatable, and nutritious (Coppock & Detling 1986; Moe *et al.* 1990; Vinton *et al.* 1993; Wilsey 1996; Gureja & Owen-Smith 2002). This effect can last for many months (Tomor & Owen-Smith unpublished). Fire alters grazing patterns and possibly it is acting to break down the positive feedback loop that maintains a grazing patch. The mechanism is described in Figure 1.1.

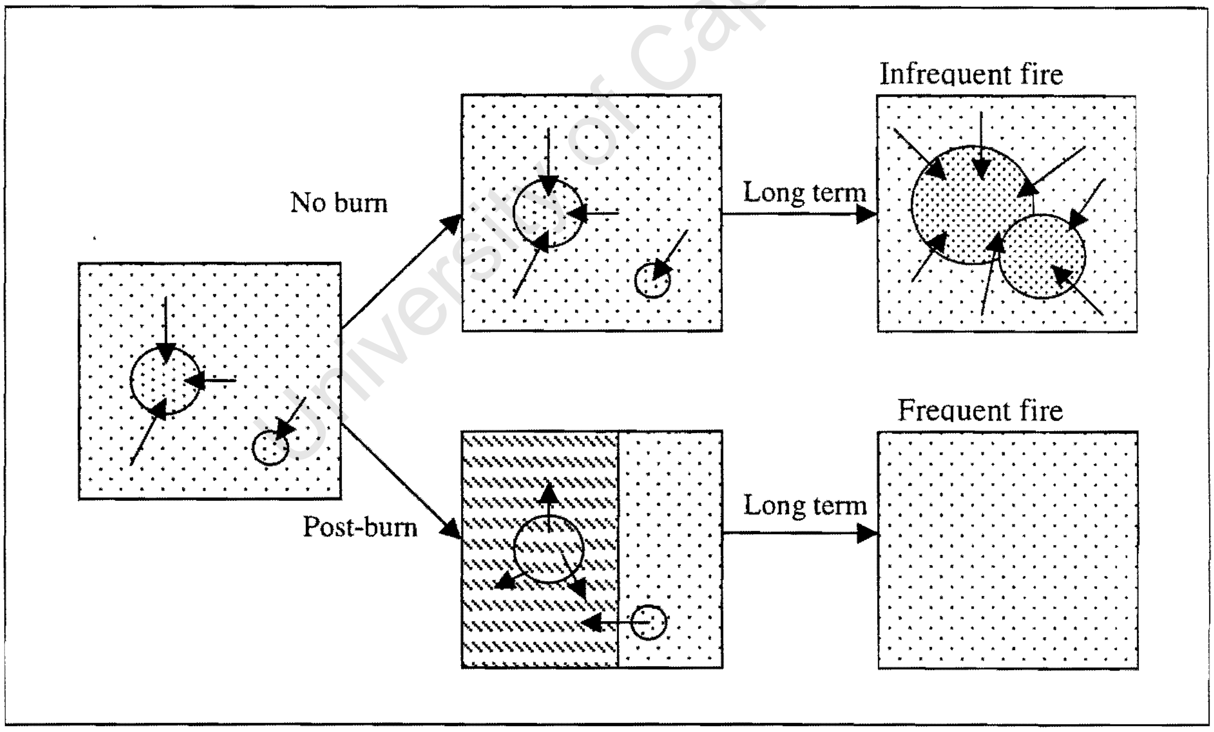

Figure 1.1: *Hypothetical effects of burning on lawn grass establishment. Animals in a bunch grass system (lightly shaded) begin to concentrate grazing on a patch. With persistent grazing, sward composition shifts to dominance by lawn grass species (heavily shaded). These expand over time if heavy grazing is maintained (low fire frequencies). After a fire, grazers move off patches into the post-burn flush in bunch-grass areas. The reduced grazing pressure allows grazed bunch grasses to recover. High fire frequencies would therefore inhibit the development of lawn grass patches by interrupting the process of continuous heavy grazing on a patch.*

There are few examples of this sort of process in the literature: Pastor *et al.* (1988), discuss how fires might increase the amount of palatable forage for moose to the extent that preferred browse species (aspen, birch, and mountain ash) grow up tall, above browse height. Coppock & Detling (1986) suggest that fires might be relieving the pressure of grazing on prairie-dog towns in South Dakota prairie grasslands. Hobbs *et al.* (1991), in a small-scale experiment, showed that fires cause grazed patches to disappear that would otherwise persist due to repeated localised grazing.

Fires and grazers, as top-down control agents in ecosystems, have been instrumental in determining the structure, dynamics, and functioning of ecosystems throughout evolutionary history (Mack & Thompson 1982; Flannery 1994; Zimov *et al.* 1995; Bond *et al.* 2003). The impacts of these agents need to be taken into account just as much as climate and soils if we are to understand and predict the how the world worked in the past, and how it will change in the future. The process that I am trying to demonstrate is an interesting example of how these two disturbances can interact/compete on a landscape level to effect vegetation change. Patterns are easy to pick up and describe, but the processes and mechanisms underlying these patterns are often intangible. In this instance, spatial interactions are the key to untangling these processes.

Thesis structure

In order to test my hypothesis I needed to show four things.

1. I needed to show that fire is indeed attracting grazers into the burnt areas; that this depletes the numbers of grazers in the unburnt areas, and disperses the grazers in the burnt areas. This would therefore prevent heavy, intensive grazing in both burnt and unburnt areas in the landscape.

2. I needed to show that this process really does cause grazed patches to disappear; that grazed patches are abandoned after fires, and that the grazed bunch grass grows up and the patch disappears. If so, I am interested in the scale of this phenomenon: over what distance is the effect of a burn apparent?

3. I needed to show that in the long term this process really did result in less lawn grass in the landscape: that areas with a history of large, frequent fires had less lawn grass than less frequently burnt areas.

4. Finally, I was interested in the dynamics of this process. If fire is acting in this way then what size fires start to have this effect? Presumably very small fires would be concentrating animals, not dispersing them. What frequency of fires is necessary to deter/obstruct lawn grass spread? How do variations in grazer density and rainfall affect this process?

Thus I designed my research in 4 parts, and report it in four different chapters in my dissertation. Each section could be seen as a study in its own right, and I have written chapters 3 and 4 as separate papers, with an introductory section to explain where they fit into my MSc as a whole.

Thesis outline

- **Chapter 1**: Introduction
- **Chapter 2** is a description of my study site: Hluhluwe Umfolozi Park.
- In **chapter 3** I describe how animal distributions are affected by fires. I compare grazer sighting data from three different years, with three different fire regimes.
- **Chapter 4** presents the results of a landscape-level experiment that I set up to test how fire affects the persistence of grazed patches in the landscape.
- **Chapter 5** is a techniques chapter, describing how I created a map of grass community types in the park from Landsat TM imagery.
- In **chapter 6** I use the map that I created and various other spatial data sets to get some insight into whether the fire history of an area has an effect on grass community proportions and distributions in the landscape; and to assess how important fire is in relation to other factors which affect grass community distributions and grazing patterns.
- In **chapter 7** I use a model to explore how the fire/grazer/grass interaction might be mediated by such things as fire size, fire frequency, rainfall and grazer density.
- **Chapter 8** is a conclusion

Technical points, definitions

I use the term *grazed patch* to refer to an area of sustained heavy grazing, which is maintained through a positive feedback between grazing and palatability; and only use the term *grazing lawn* to denote a grazed patch that has a different species composition from the surrounding un-grazed landscape. The term *grazing lawn* has been used in both senses in the literature (McNaughton 1984; Drent & van der Wal 1999) but in my thesis a *grazing lawn* is an area dominated by stoloniferious "*lawn grass*" species, as opposed to caespitose "*bunch grass*" species.

The distinction is important because a grazing lawn is a specific habitat type, whereas a grazed patch is different from the rest of the landscape due to structural differences alone, and thus is much more ephemeral: if the grazed bunch grass gets the opportunity to grow tall, and become less palatable, the grazed patch will disappear. Bunch grasses grow very fast. Rangeland studies have shown that, depending on the time of year, they can fully recover from a release of grazing pressure within 6 weeks to 3 months (Scott 1959; Danckwerts & Aucamp 1985; Danckwerts & Nel 1989; Vallentine 1990).

Chapter 2: Site description

Hluhluwe Umfolozi Park is a mesic savanna system in Northern Kwa-Zulu Natal, South Africa. It is situated about 40km from the coast: 28°00'- 28°26' S, 31°43' - 32°09' E (Figure 2.1). It is a system of around 90 000Ha with a varied topography: altitude ranges from 40m to 750m above sea level. It consists of rolling hills and valleys, tending towards undulating lowlands in the south and west (Plate A). Altitude and rainfall tend to decrease from the North-East (Hluhluwe) to the South-West (Umfolozi).

Mean minimum temperature is 13° C and mean maximum temperature is 35° C. Frosts are rare. Mean annual rainfall ranges from c. 600 to c. 1000mm pa, generally increasing with altitude (Balfour & Howison 2003). Annually, rainfall shows a unimodal seasonal pattern and the driest time of year is between June and August. Hluhluwe Umfolozi Park is typical of Southern African savannas in that it is prone to long-term fluctuations in rainfall. Extended periods of above average rainfall are followed by periods of below-average rainfall (Brooks & Macdonald 1983; Balfour & Howison 2002, Figure 2.2). These periods last on average between 4 and 10 years (Balfour & Howison 2003).

Soils in the park are derived largely from shales and sandstones, which are intermittently fractured with extensive doleritic intrusions (King 1970; Graham 1992). There are small areas of older granite-gneiss formations in the west, and some basalt along the eastern boundary. The distribution of soil-types is related to the underlying geology (Graham 1992). Predominant upland soils are Hutton, Shortlands, Glenrosa, Mispah, Mayo and Milkwood; and bottomland soils are Oakleaf, Valsrivier, Fernwood, Bonheim and Inhoek.

Vegetation ranges from grasslands, to *Acacia*-dominated savannas to broad-leaved thickets. Some forests occur in areas of higher rainfall (high elevation), and in areas protected from fire. Most of the park is savanna woodland, with varying amounts of woody cover (Plate B). Tree-densities have been increasing since the 1950's and many of the open grassland communities are encroached by short, shrub-like *Acacia karroo* and *Dychrostachys cinerea* plants, which are kept short because of frequent burning. The area is classified by Acocks (1988) in the Zululand Thornveld Coastal Tropical Forest veld type and in the Lowveld Tropical Bush and Savanna veld type. Wateley & Porter (1983) give a comprehensive account of the vegetation in the park.

There is a much less pronounced association of soils and vegetation at HUP than in other savanna systems, partly because the soils and geology are quite varied (King 1970), and also because much of the area is too hilly to generate the catenary sequences found in old African landscapes (Bond *et al.* 2001). However, there is still a range of grass communities represented in the park.

The most prevalent grassland types are bunch-grass communities, dominated by andropogonoid grasses, especially *Themeda triandra*, *Cymbopogon* spp, *Hyparrhenia filipendula, Heteropogon contortus* (Downing 1974; Brooks & Macdonald 1983, Plate C). Other bunch grass communities are also present however, especially *Sporobolus pyramidalis/Eragrostis curvula* communities. Bunch grasses are tall, tussock-forming grasses, which grow very fast, produce a high fuel load (400-700gm^{-2}), and promote frequent fires. These tall-grass areas do not support high numbers or a high diversity of grazing animals; only Buffalo (*Syncerus caffer*) is a tall grass specialist at Hluhluwe (Page & Walker 1978). Bunch grasses are also fairly intolerant of heavy grazing - their growth-form means that their leaves are not protected from grazing, and they cannot reproduce vegetatively (Plate E). They are mostly of decreaser/increaser I ecological status (Tainton 1999). Thus these grass communities are most dominant in areas of frequent fire and relatively low grazing pressure.

However, "grazing lawns" – areas of intensive grazing dominated by grazing-tolerant grass species – do occur at HUP (Plate D). The grass species in these areas are short-statured, stoloniferous grasses that spread mainly through vegetative growth and are tolerant of, and productive under, heavy grazing (Plate F). These areas in the park appear to be associated with higher numbers of animals, and a more diverse grazer assemblage: at Hluhluwe Umfolozi Park, Impala (*Aepyceros melampus*) , White Rhino (*Ceratotherium simum*), Zebra (*Equus quagga burchelli*), Wildebeest (*Connochaetes taurinus*), Nyala (*Tragelaphus angasi*), and Warthog (*Phacochoerus africanus*), are all associated with grazing lawns (ZLGP data – still being collected).

History of the park

Hluhluwe and Umfolozi Game Reserves were proclaimed in 1885. The two parks were joined together by incorporating the corridor area (Figure 2.1), and fenced, and have been managed as a single entity since the early 1970's.

Animal numbers

Grazer numbers at HUP have been very variable. Late in the 19th century and in the early part of the 20th century the populations crashed from nagana and rindepest outbreaks, and then from disease-control campaigns, which resulted in heavy culling. However, animal numbers also increased fairly quickly when protection measures were put in place (Brooks & Macdonald 1983).

In more recent years, when the park has been managed for game, it is estimated that grazer biomass has ranged from 54kg/Ha (0.12LSU/Ha) to 133kg/Ha (0.29LSU.Ha) (Brooks & Macdonald 1983). After a severe drought in the early 1980's there were extensive game removals (in line with management's 'tracking' policy of population control in response to climate), and animal numbers remained low until the 1990's (Olff 2000). Reliable animal censuses have been conducted through an EarthWatch program since 1990 and these give the present grazer biomass for the whole park to be about 90kg/ha (0.19LSU/Ha) – about the recommended stocking density on commercially managed cattle farms in this region (Tainton 1999).

Fire management

Both fire frequency and the proportion of area burnt have been very variable at HUP since the 1950's, when fire records were first collected (Balfour & Howison 2003). The frequency and size of fires are affected both by variation in fuel loads during wet and dry periods of rainfall, and by fire management policies. The latter have shown a dramatic shift from trying to reduce/minimise fire in the park, to active burning policies aiming to control bush encroachment (Brooks & Macdonald 1983). Thus the area of the park that burns in a year has ranged from 0 to 80~~0~~ 000 Ha (90% of the park). In recent years there has been a general increase in area burnt and at present (except in extreme drought years) between 30 and 50% of the park is burnt in any one year (Figure 2.3). The mean fire return period for any area in the park is 3.8 years, but this is highly skewed towards the shorter fire return intervals, and the median fire return period is only 1.3 years (Balfour &

Howison 2003). Most of the fires (both management fires, and accidental burns) occur in August/September (Balfour & Howison 2003).

Grass layer

Various lines of evidence suggest that extent of lawn-grass-dominated areas has decreased considerably since the 1970's (Bond *et al.* 2001): aerial and fixed-point photographs show that areas that were grazing lawns are now dominated by bunch grass species like *Sporobolus pyramidalis*. It is possible that low grazer numbers in recent years have resulted in this decrease in lawn grasslands, which are created and maintained by heavy grazing (McNaughton 1984). Increased rainfall and fire frequencies during this time could also have contributed towards the decrease in lawn grass communities. There is evidence therefore that HUP is a highly dynamic system and that the proportions and distributions of different habitat types (grass and tree communities) are very variable, depending on factors such as grazing, fire, and rainfall.

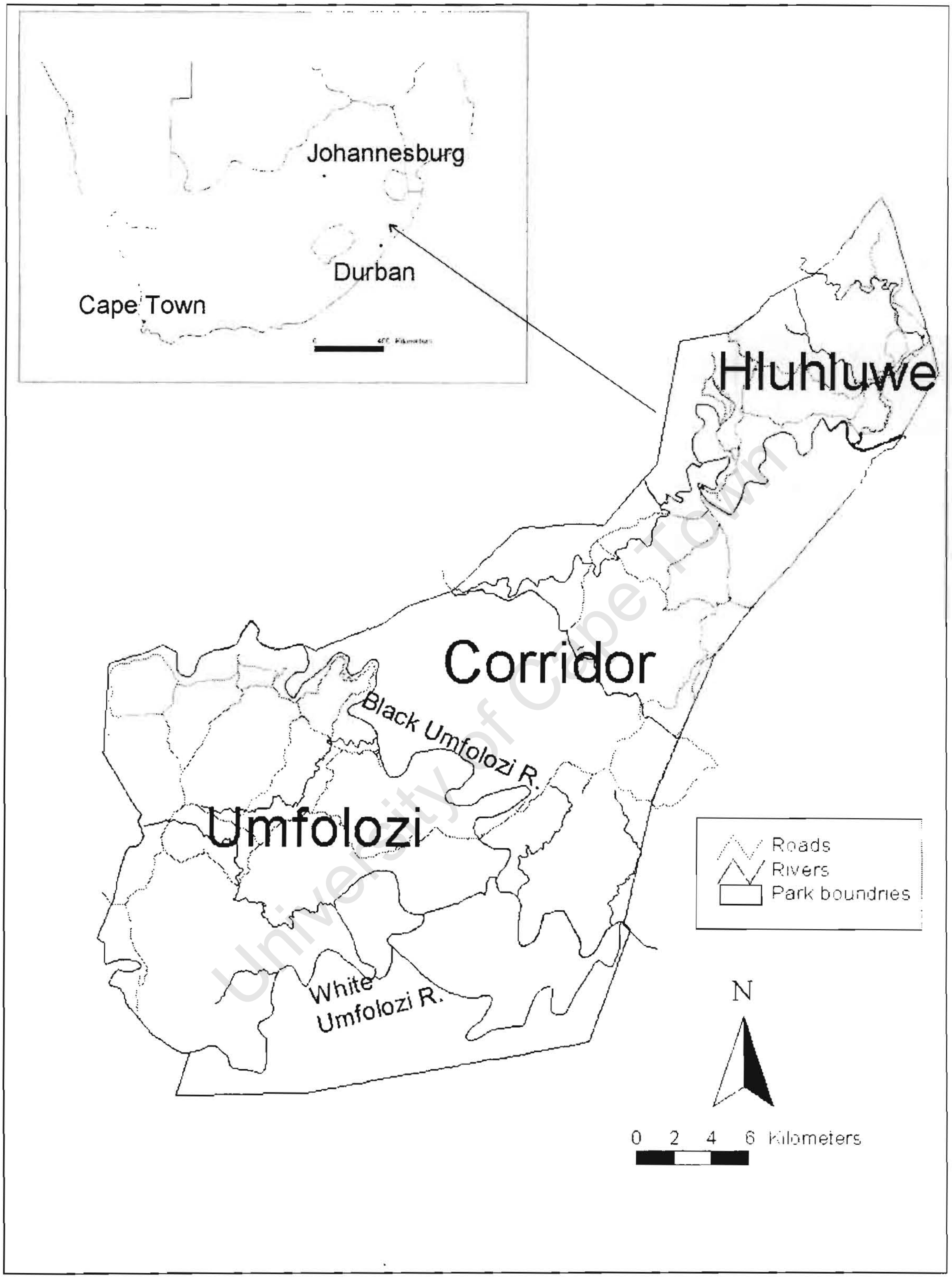

Figure 2.1: Map showing the location of Hluhluwe Umfolozi Park, the major rivers, roads and sections of the park.

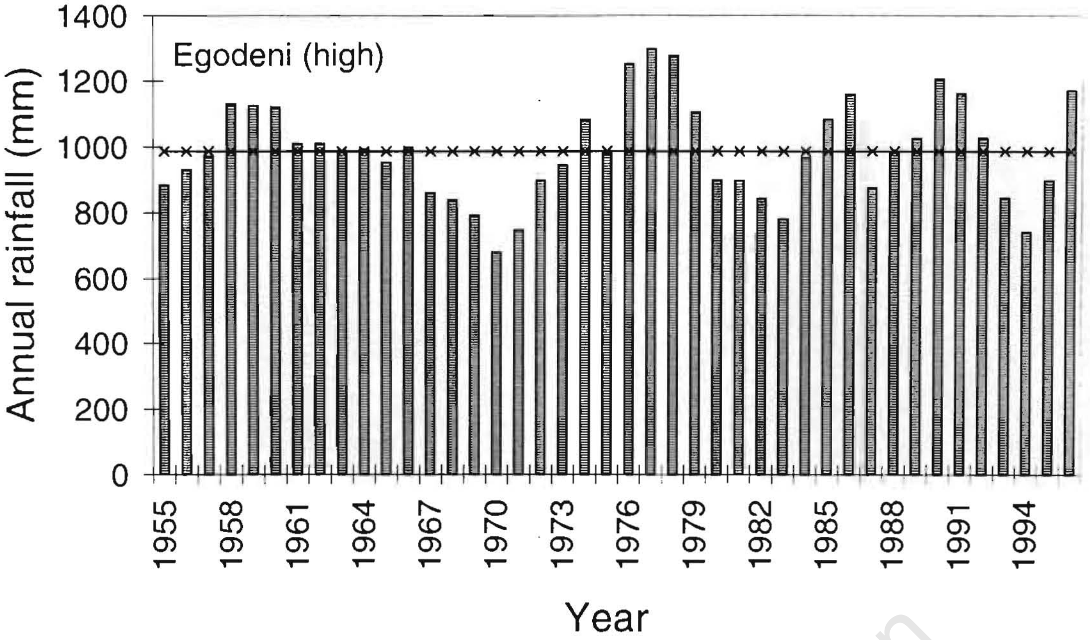

Figure 2.2: Three year cumulative rainfall and long term mean for the years 1956 to 1996 at Hilltop Camp (High rainfall northern region of Hluhluwe Umfolozi Park). Data from (Balfour & Howison 2003). Low rainfall southern regions show similar long-term fluctuations around a mean of 700mm.

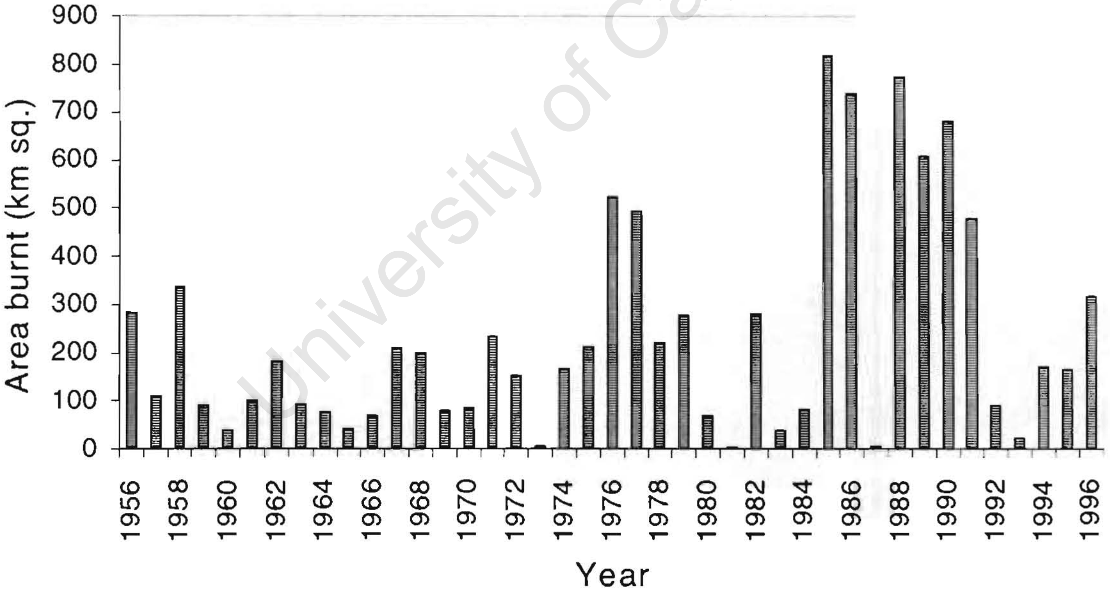

Figure 2.3: The annual area burnt in Hluhluwe-Umfolozi Park (km^2) for the period 1956 to 1996. Data from (Balfour & Howison 2003). (Total area of park is $900km^2$).

PLATE A: *A view of Hluhluwe Umfolozi Park from a high-lying hilltop in Hluhluwe*

PLATE B: *Savanna woodland at HUP. Much of the park is covered with savanna woodland with varying degrees of tree cover.*

PLATE C: *A typical andropogonoid bunch grass community*

PLATE D: *Lawn grass community (Grazing Lawn)*

Plate E: *Bunch Grass growth form: response to heavy grazing*

Plate F: *Lawn grass growth form: response to heavy grazing*

Chapter 3: preface

The aim of this chapter was to show how animal distributions in the park are affected by annual fires. Although grazers have been shown to be attracted to post-fire regrowth in many grazing systems throughout the world, it was important to my hypothesis to be able to show that this was occurring at Hluhluwe Umfolozi Park too. I also wanted to highlight two aspects of this process: firstly, the impact that it has on the grass layer – that after fires both burnt and unburnt grassland is exposed to different levels of grazing; and secondly that fire alters patterns of grazing on a smaller scale - within a burn - as well as on a larger scale - over the whole landscape.

Chapter 3: Grazer movements in relation to fire at Hluhluwe-Umfolozi Park

Introduction

In grassland and savanna systems all over the world it has been noted how grazing animals are attracted to the green regrowth after a fire (Coppock & Detling 1986; Moe *et al.* 1990; Vinton *et al.* 1993; Wilsey 1996; Tomor & Owen-Smith unpublished). Post-fire regrowth is of much higher forage quality than unburned grassland because it has both a higher intrinsic nutritive value and a higher bulk density (van de Vijver 1999). Thus fire has been used by hunters, pastoralists, and commercial farmers for many years to manipulate animal movements and to provide good forage (Hall 1984).

Research into this process has focussed on individual species' responses to fire. Most grazers – even long-grass specialists – are more abundant in burnt than in unburnt vegetation after fires (Wilsey 1996; Gureja & Owen-Smith 2002), and this effect can last for several months, well into the growing season (Nellis & Briggs 1989; Tomor & Owen-Smith unpublished). However, we have very little information on the spatial context in which this is happening, or how this process affects landscape patterns of grazer movements.

In systems where animals move freely through a landscape, the distribution of grazing in the landscape is largely dependent on the distribution of optimal feeding resources, and the distribution of water (Laca & Demment 1991; Bailey *et al.* 1996; Drent & van der Wal 1999; Brock & Owensby 2000). Because it has such an impact on the distribution and availability of high-quality forage at certain times of the year, it follows that fire would be one of the major factors which is determining annual grazing patterns.

Most factors which control grazer distributions, such as rainfall, temperature, the distribution of water points, and predation risks, vary fairly predictably in space and time; and the movement patterns of various grazer species have been described in relation to this variability (Talbot & Talbot 1963; Pennycuick 1975; Sinclair & Norton-Griffiths 1979; Pearson *et al.* 1995). However, the timing, size, and distribution of burns can be very different from one year to the next. At Hluhluwe Umfolozi Park, Kwa-Zulu Natal, research is showing that buffalo will alter their home ranges annually depending on the burns of the previous year (Jolles, pers comm.), and there are records of many species moving out of their normal sub-population areas during the fire season (Brooks 1981).

Thus burning is likely to be accounting for much of the variation that we see in grazing patterns, but we have very little understanding of how this operates in the landscape. It is of interest to us not only whether animals move into the post-fire green flush, but how this alters the patterns of grazing in burnt and adjacent unburnt areas.

This question is important because vegetation is strongly affected by both the frequency and the intensity of grazing (O'Connor 1985; O'Connor 1994; Knapp *et al.* 1999; Lemaire *et al.* 2000; Weber *et al.* 2000). How long, and how heavily an area is grazed may have a large impact on the grass communities, and therefore the habitat-types in the area. This has been demonstrated very clearly in research in rangeland systems. In these systems, the aim is to determine the most productive, sustainable way to distribute cattle in the landscape over the year (Tainton 1999). In game reserves and national parks the frequency and intensity of grazing is also affecting grass communities, but the distribution of grazers in these systems is controlled not by fences, but by internal ecological processes. Of these processes, fire is one that it is necessary to manage, and it is important to understand how it is operating.

So how are fires altering grazing patterns? Are they dispersing grazers in the landscape or concentrating them on smaller patches? From what distance can fires attract grazing animals, and what would grazing patterns through the growth season look like in the absence of fire? It is quite difficult to answer these questions. Accurate spatial information on the distribution of herbivores over time is difficult and expensive to collect, and it is also not easy to manipulate fire in these systems.

Hluhluwe-Umfolozi Park (HUP) in Northern Kwa-Zulu Natal provided an opportunity to investigate spatial questions around the effect of fires on grazers. It is a mesic savanna system, 90 000 Ha in area, with a wide variety of grazing animals: zebra, wildebeest, buffalo, white rhino, impala and warthog (See Brooks & Macdonald (1983) for a description of the area). A large proportion of the park is burnt every year (sometimes more than 60%) and there is digitised data on the dates and spatial distributions of fires each year. Spatial information on the distribution of herbivores is also gathered every second year: a game census (funded by EarthWatch) is conducted by walking 26 transects in the park, recording the location of all animals sighted.

I used this data and GIS software to investigate the patterns of grazing at HUP over the fire season for three years: 1996, 1998 and 2000. Each year had a very different fire regime. Using this data I aimed to describe the patterns of grazing each year in the context of the spatial and temporal patterns of burning. I also wanted to answer three main questions:

1. Are animals attracted to the post-fire green flush at Hluhluwe-Umfolozi Park? If so one would expect to find more grazing animals in the areas that had been burnt than would be expected based on the proportion of burnt areas in the park.

2. What does this mean for the areas that are not burnt? How different are the grazing patterns each year in areas that have not been burnt, and can these differences be explained with reference to the fire regime, and the spatial context of these areas within a burnt landscape? It would be expected that, depending on the timing and distribution of fires in the surrounding areas, unburnt areas would be depleted of grazing animals as the fire season progressed.

3. Are animals distributed differently in burnt areas? Grazing creates heterogeneity in a landscape (Briggs *et al.* 1998; Adler *et al.* 2001; Fuhlendorf & Engle 2001): patches that are initially grazed are often re-grazed (Drent & van der Wal 1999), and a patchy mosaic of palatable (short) and less-palatable (tall) grasses can develop. However, fire has a homogenising influence on a landscape (Hobbs *et al.* 1991), after burns any heterogeneity caused by grazing is eliminated and the entire area consists of uniformly short, new regrowth equally palatable to grazers. Therefore it is expected that grazing patterns would be very different in burnt areas and that animals would be spread more evenly through the environment.

Thus I was investigating the effect of fires at two scales: firstly on the scale of the entire park, I was interested in how the increase in high-quality forage after burns affects grazer movements, and whether the size, distribution and timing of fires are important factors mediating this effect. Secondly, at a smaller scale, fire has a homogenising influence on the landscape. I was interested in whether this can alter inherently patchy patterns of grazing, and create a more uniform grazing environment in the burnt areas.

Methods

Study Area

Some portions of the present Hluhluwe Umfolozi Park have been managed as game reserves since 1895, but the present extent of the park was only proclaimed and fenced in by the early 1970's (Brooks & Macdonald 1983). Thus, this 90 000 Ha area has been managed as a single system, within which grazing has been contained, for about 20 years. The only management of herbivores in this park has been culling and removals. The park has a high diversity of herbivores (Appendix 1), and has a varied topography. Altitudes range from 40 to 750m and rainfall ranges from c. 600 to c. 1000mm p.a.

Hluhluwe is a mesic savanna system. Rainfall shows a clear seasonal pattern with a wet season from October to May; and rainfall and altitude both tend to decrease from north to south. There is a prominent woody component, especially in the north, which is dominated by Acacias (Brooks & Macdonald 1983). Much of the grassland areas of the park are tall, bunch grass communities. Dominant species are *Themeda triandra, Sporobolus pyramidalis, Eragrostis curvula,* and *Hyparrhenia filipendula.* These communities produce a large standing biomass each year (up to 700 gm^{-2}), and are highly flammable. A smaller proportion of the park consists of grazing lawn areas which are dominated by shorter-statured, palatable grasses, including *Urochloa mosambicensis, Digitaria longiflora, Panicum coloratum* and *Sporobolus nitens.*

Grazing tends to be concentrated in the lawn grass areas during the wet season, but in the dry season, when there is no more growth on the grazing lawns, many grazers do move into the tall grass areas and start to graze the available biomass (Melton 1987; Owen-Smith 1988). However, grazing continues to be patchy, because once a tall grass area has been grazed short it tends to get re-grazed. Management fires are generally set towards the end of the dry season, and therefore, if they are attracting grazers, they would be disrupting this pattern of patchy dry-season grazing. The impact of fires on these grazing patterns is what I aimed to investigate.

Data collection

Most burns occur at the end of the dry season between July and October. The management blocks that burn are recorded by field-rangers, together with the date and intensity of the burn. Digitised fire maps for each year are created from hand-drawn field maps at the research station in the park. These maps therefore represent blocks that a fire passed through, rather than showing the exact patches that burnt. These maps were imported into ARCVIEW as shape-files (Figure 3.1).

Spatially explicit game count data has been collected every 2 years since 1996 as part of an EarthWatch program. Trained field assistants walk 10 km transects early in the morning (between 5am and 8am). There are 26 transects that are evenly spaced throughout the park (Figure 3.1), except in the wilderness area, which is sampled in a different fashion and not included in our study. The position of any herbivores sighted within 500m of the transect is recorded by measuring the bearing and the distance from the transect and the distance along the transect (accurate to the nearest 100m). Field assistants also record the species, number of animals, vegetation type (broad structural categories), and whether the animals were sighted in a burn or not. I imported this data into ARCVIEW and made it spatially explicit by linking it to a shape file of the walked transects using ARCVIEW's geocoding functions. The product was a point file (accuracy 100m-500m) of all animal sightings, linked to a table containing information about each sighting.

Transects are walked over a period of about 8 weeks between August and October (this varies slightly between years, see Table 3.1 for details), each transect is walked between 12 and 15 times during this period (Table 3.1). Thus there is detailed information on the positions of herbivores throughout the park over the period of the fires, but this does not continue into the dry season. Also, a certain percentage of the park had already burnt before the transects were started for all three of the sampling years (Figure 3.1), so there is no clear pre-fire data available.

This information can be used to investigate the effect of fires on herbivore distributions at the end of the dry season, but there is no information available on how this fits into seasonal patterns of herbivore movements. The data is difficult to work with because the transects were all walked different numbers of times, on different dates; and because for two of the years the fires continued through the transect walks, meaning some transects were sampled before and after they were burnt.

Table 3.1: Describing the sampling regime for game count data over the three years of the study.

	1996	1998	2000
Transect start date	2-Sep-96	26-Aug-98	5-Aug-00
Transect end date	20-Oct-96	21-Oct-98	9-Oct-00
total number of transects walked	354	354	370
minimum number of walks per transect	12	12	11
maximum number of walks per transect	15	15	17

Table 3.2: Total numbers of grazing species for the three study years (data from HUP research station calculated from game count data using DISTANCE software).

	1996	1998	2000
Buffalo	4240	4530	2865
Impala	16415	16723	24827
Nyala	5939	7406	9543
White rhino	1364	1542	1687
Waterbuck	891	653	792
Warthog	1745	2164	4072
Wildebeest	2730	2381	3364
Zebra	3012	3282	3124

Data analysis

Data were analysed in a number of ways to answer the three questions about grazer movements.

1: Proportions of animals in burnt and unburnt areas:

For each year, to see whether burnt areas had relatively more grazers than unburnt areas I calculated the total area of all sections of the transects that were burnt before the game counts, and the total number of sightings in this area. I also calculated total area and total sighting number for all sections which remained unburnt throughout the game count period. I used number of animal sightings instead of number of animals to ensure that all observations were independent (Coppedge & Shaw 1998). Use of sighting number as opposed to number of individual animals is justified because the average numbers of animals per sighting for each species did not change with time, or after the burns (Chi Square $p<0.001$). Instead of using all the data (sightings from within 500m on either side of the transect), I only used sightings that were within 20m of the transect so as to ensure that there was no bias in favour of burnt areas because of improved visibility at a distance. For each year, using the total number of sightings, and the total area of burnt and unburnt transects I calculated the expected numbers of sightings in the burnt and unburnt areas based on their relative proportions in the park, and ran Chi-Square tests to see whether there were more observed sightings in the burn than would be expected.

2: How unburnt areas are affected by surrounding burns:

To look at how grazing numbers in unburnt areas change as a result of neighbouring fires I compared unburnt areas between the three years. I isolated all portions of the transects which had remained unburnt in all three years, and calculated the average number of sightings per walked transect for each year. I only used transects in which >200Ha had remained unburnt because smaller areas were too patchy. Thus the animal numbers on the same section of transect could be compared between years in the context of the timing and distribution of fires, which varied between the years. Each transect was used as an independent replicate and a sign test was performed to see whether some years had consistently fewer sightings than other years.

For each year I also looked at temporal changes in animal numbers in the unburnt areas over the time of the census. As more of the park burns, it is expected that fewer and fewer animals would be found on the unburnt areas. For each year I isolated areas which had not been burnt that year. I extracted the total numbers of sightings on a transect each date the transect was walked. Then I tested to see whether number of sightings was correlated with date, using each transect as an independent sample (I excluded transects with unburnt areas of less than 300Ha).

3: Distribution of grazers in burns

I used various methods to look at the change in spatial distributions of animals in burnt areas.

Descriptive data

As mentioned earlier, the way that the data was collected makes it difficult to isolate comparable situations. However, there *were* a few transects that were entirely burnt or entirely unburnt on different years, and one transect that was burnt in the middle of the sampling session. It was possible to use these transects to describe the changes in animal distributions in burnt areas

Quantitative analysis

In order to quantify how clumped or dispersed animals are in the landscape I dissected the transects into segments and counted the numbers of sightings in each of the segments. If animals are clumped it would be expected that some of the transect segments would have many sightings, and others would have fewer sightings: i.e. that the data would be more dispersed around the mean. If animals are evenly spread throughout the landscape, the number of animals found in different segments along the transect should be less variable. I used the coefficient of variation (CV= st.dev/mean) to quantify this variability (see Figure 3.2 for an illustration of this measure of clustering)

However, first it was necessary to isolate areas in the park that were comparable i.e. burnt one year and not burnt the next. Using GIS tools and the three fire maps I isolated:

- all the areas that were burnt in 1996, and unburnt in 1998 and 2000,
- all the areas that were burnt in 1998, and unburnt in 1996 and 2000,

I extracted the relevant sighting information from these data sets. Very few areas were burnt before the game counts in 2000, so I was not able to compare all the areas that were burnt in 2000, and unburnt in 1996 and 1998.

I cut the transects up into 500m segments and calculated the total number of sightings per segment. From this I could calculate the CV for each transect for each year, then compared the CV between years for each of the data sets.

Results

Comparing the fire regime between years

As can be seen from Figure 3.1, there is a great deal of variation in the area and timing of fires between the three sampling years. Figure 3.3 shows how the cumulative area burnt changed with time for each of the sampling years. In 1996 most of the fires (about 30 000Ha) had already occurred before the game counts started on the 2nd September, whereas in 1998 a much smaller area was burnt when the transect walking started. It was only by the 9 October 1998 that an area equivalent to 1996 had been burnt. In 2000 the amount burnt before the game counts was very small (7600Ha), but this increased rapidly all the way through August, September and October until the total area burnt was much larger than in 1996 or 1998. These differences are shown in Figure 3.4.

Rainfall, another factor which could potentially be affecting the forage resource and therefore influencing animal movements, was fairly similar between years over the time of the transect walking (Figures 3.5 and 3.6). There was slightly more rainfall during the dry season in 1996 than in the other two years, and the total amount of rainfall that had fallen by the end of October ranged from 178mm (1996) to 133mm (2000)

Thus (while I have no data set representing a non-fire situation) these three years allow me to

1: compare grazer distributions in situations where a large area of the park is burnt and situations when a smaller total area burnt (1996/2000 : 1998)

2: to look at how the grazing patterns change over the season as the area burnt increases (2000: 1996/1998).

Testing grazer preference for burns

Table 3.3 shows the results of a chi-squared test for differences from the expected numbers of animal sightings in burnt and unburnt areas for each year. Significantly more grazers were recorded in the burnt areas than would be expected if they had been randomly distributed with respect to burning in 1996 and 1998. In 2000 this result was reversed, but this data is unreliable because of the very small proportion of the transects which had burnt before the game counts (only 48Ha). Therefore grazers are attracted to the burnt areas in HUP.

Table 3.3: *Chi-squared test comparing total number of sightings in burnt and unburnt sections of the transects for 1996, 1998, and 2000. Only the sections that were burnt before any of the transects were walked, and the sections that were unburnt throughout the entire census period were included in the analysis.*

		total sighting area (Ha, 20m buffer)	number of grazer sightings			X^2	significance
			observed	expected	O-E		(df=1)
1996	burnt	264.03	295	213	82	31	
	unburnt	547.62	361	443	-82	15	
	total	**812**	**656**	**656**	**0**	**46**	**0.001**
1998	burnt	220	278	239	39	6	
	unburnt	483	487	526	-39	3	
	total	**703**	**765**	**765**	**0**	**9**	**0.01**
2000	burnt	42	29	43	-14	4	
	unburnt	358	378	364	14	1	
	total	**400**	**407**	**407**	**0**	**5**	**0.05**

Differences in grazer numbers in unburnt areas between years

To test whether grazer numbers in unburnt areas are reduced in years when more of the park was burnt, I compared grazer presence (measured as the average number of sightings per walked transect) for sections of transects that were unburnt in all three years (Table 3.4). Less of the park was burnt in 1998 than in 1996 or 2000 (Figure 3.3), and the average number of animals per unburnt walked transect was generally greater in 1998 than in 1996 and 2000. There were no significant differences between 1996 and 2000.

Table 3.4: *A - Average number of sightings per section of unburnt transect for the three study years. The values are then ranked from smallest to largest. B –results of a sign test for differences between years.*

A

Transect number	**Area unburnt** (Ha)	**Average number of sightings**			**Rank**		
		1996	**1998**	**2000**	**1996**	**1998**	**2000**
2	750	0.4	1.1	0.6	3	1	2
3	300	1.1	4.1	2.0	3	1	2
4	200	0.1	1.2	0.0	2	1	3
6	337	1.6	2.5	1.8	3	1	2
10	208	0.2	0.4	0.1	2	1	3
15	696	6.3	5.9	4.8	1	2	3
16	289	0.8	0.9	1.1	3	2	1
17	716	4.8	5.1	3.9	2	1	3
20	309	5.3	3.8	2.1	1	2	3
21	613	13.2	14.6	12.1	2	1	3
22	397	2.5	4.4	3.4	3	1	2
23	302	4.1	5.4	0.8	2	1	3
24	250	1.8	3.2	1.1	2	1	3
25	340	4.4	3.3	4.5	2	3	1
26	291	4.3	3.2	2.3	1	2	3
				Sum of Rank	**32**	**21**	**37**

B

	2000<1998	1996<1998	2000<1996
total yes	13	11	9
total no	2	4	6
Total replicates	15	15	15
significance	**p=0.004**	p=0.059	p=0.304

Changes in grazer numbers over time in unburnt areas

If burnt areas attract animals away from unburnt areas then the number of sightings on unburnt census transects should decrease as the fire season progresses, and should decrease more strongly in years when large areas are burnt.

Correlations between sighting number and date of sampling are shown in Table 3.5. In 2000 - when the amount of the park burnt was increasing very rapidly during the transect walking - 36% of the transects showed a significant decrease in numbers of sightings with time, and all except 1 of the 14 transects showed negative trends of sightings with time. In 1996 - when the amount of the park burnt did not change during the transect walking - sighting numbers in the transects showed both positive and negative trends with time (13 negative, 7 positive). 1998 - where the amount of park burnt stayed smallest for longest, but did increase rapidly at the end - was more similar to the pattern in 2000.

Table 3.5: *Correlation coefficients of total number of sightings vs. date for unburnt sections of the transects for the three study years. The number of Ha of the transect that were unburnt is shown in the area column: transects with less than 300Ha unburnt were not included. Bold values are significant (p<0.05)*

	1996			**1998**			**2000**		
Transect number	area	n	r	Area	n	r	area	n	r
2	841	13	-0.34	799	13	0.13			
3	750	13	**0.65**	449	13	-0.83			
5	826	12	-0.56	471	10	-0.44	599	12	-0.12
6	590	14	-0.38				458	12	-0.31
10	503	13	0.80	603	13	-0.3	522	12	-0.18
11	765	14	-0.01	927	15	0.17			
12	569	13	**0.59**	398	14	0.29			
13	462	13	0.16	612	14	-0.26	469	11	**-0.49**
14	346	13	-0.35	636	13	**-0.70**	304	12	**-0.84**
15	768	12	0.31	817	13	**-0.64**	626	11	**-0.65**
16	401	11	0.32	733	13	0.35	731	13	**-0.64**
17	716	15	-0.17	350	13	-0.36	477	10	-0.43
19	612	15	-0.11	716	14	-0.34			
20	727	15	-0.13	915	13	**-0.56**	716	14	**-0.66**
21	613	13	**-0.72**	819	14	-0.03	512	16	-0.29
22	836	13	-0.28	411	12	-0.16	976	17	-0.28
23	752	14	-0.45	785	14	-0.04	626	13	-0.2
24	901	14	-0.29	881	13	-0.14			
25	974	15	-0.45	870	15	-0.45	505	15	-0.29
26	791	12	0.38	328	5	-0.21	458	14	0.05
No. of significant negative correlations			1 (5%)			3 (16%)			5 (36%)

Spatial patterns in the burnt areas

Figure 3.7 shows the distribution of Impala, Zebra, Wildebeest and White Rhino along Transect 11 on all of the dates that it was walked in 2000. Transect 11 was burnt halfway through the census period on the 31st August. After the fires the animals were spread out over much more of the transect than they were before the fires. A similar pattern is shown between years for Transect 8 (Figure 3.8). This transect was burnt in 1996 and 1998, but unburnt in 2000. The animals were only found in a small section of the transect in 2000, whereas they were spread quite evenly in the other two years. Both of these transects run through undulating, predominantly tall-grass country; the type of area that would be much more attractive to grazers after it was burnt.

No statistical tests could be done on these results because these were the only two transects that were entirely within or without a burnt area on comparable years. The rest of the transects were all burnt in portions and fragments.

Figure 3.9 compares the average CV of sightings for the same section of transect in burnt and in unburnt years. The CV is generally lower in the year when it was burnt than in the other two years, (i.e. animals are dispersed more evenly through the landscape), but these differences are not statistically significant (too few replicates).

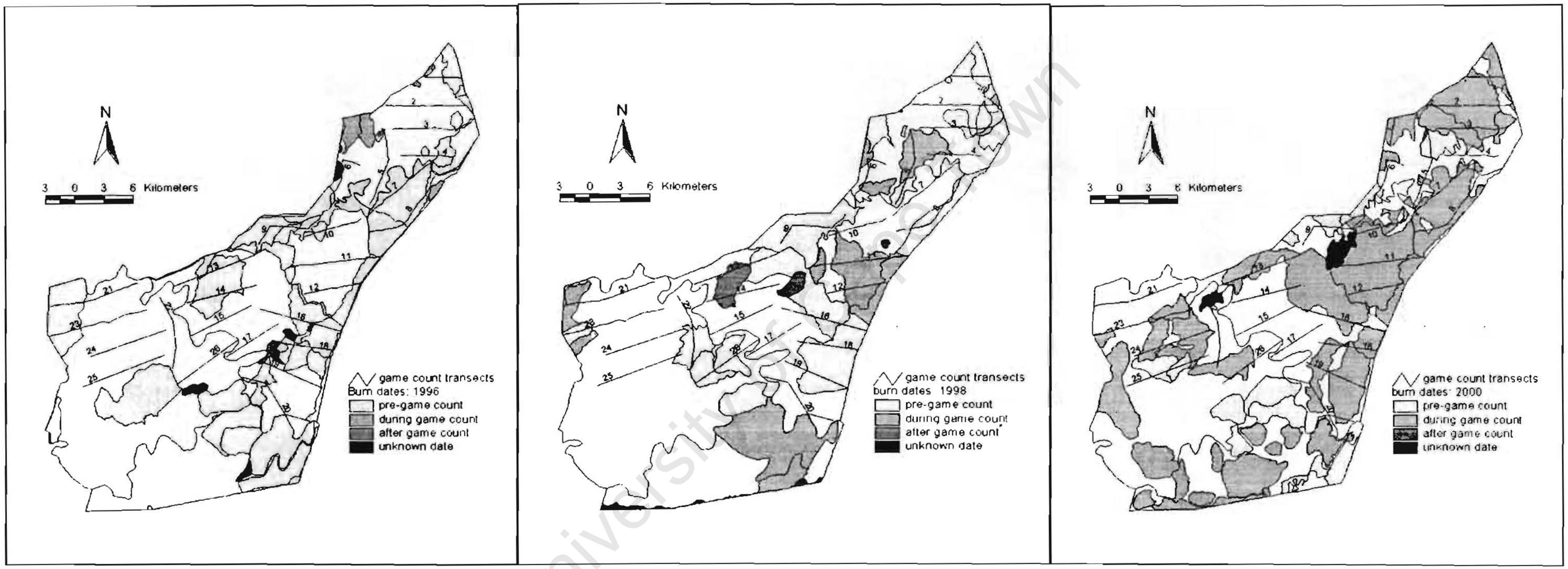

Figure 3.1: *Areas and dates of the fires in 1996, 1998 and 2000 at Hluhluwe Umfolozi Park, Kwa-Zulu Natal*

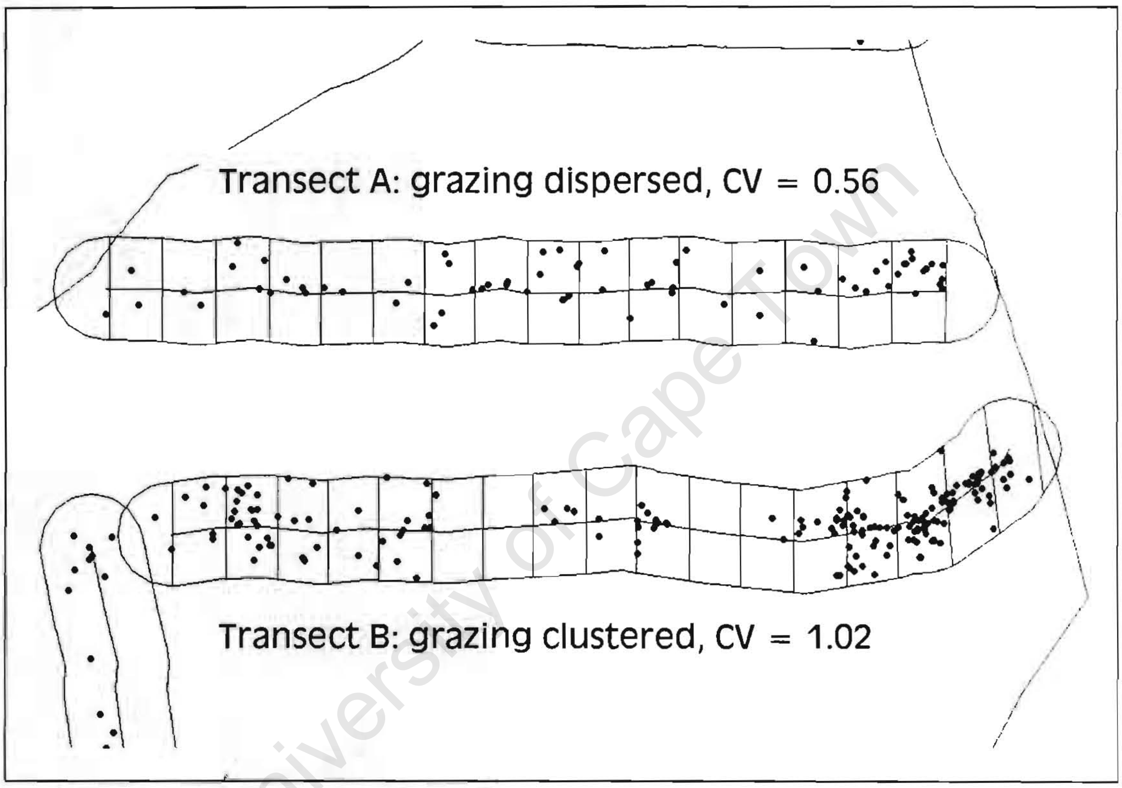

Figure 3.2: *Diagram showing how a measure of the CV (stdev/mean of animal sightings in 500m segments along a transect) can distinguish between a dispersed and a clustered pattern of grazers. This measure is independent of the total number of sightings in the transect.*

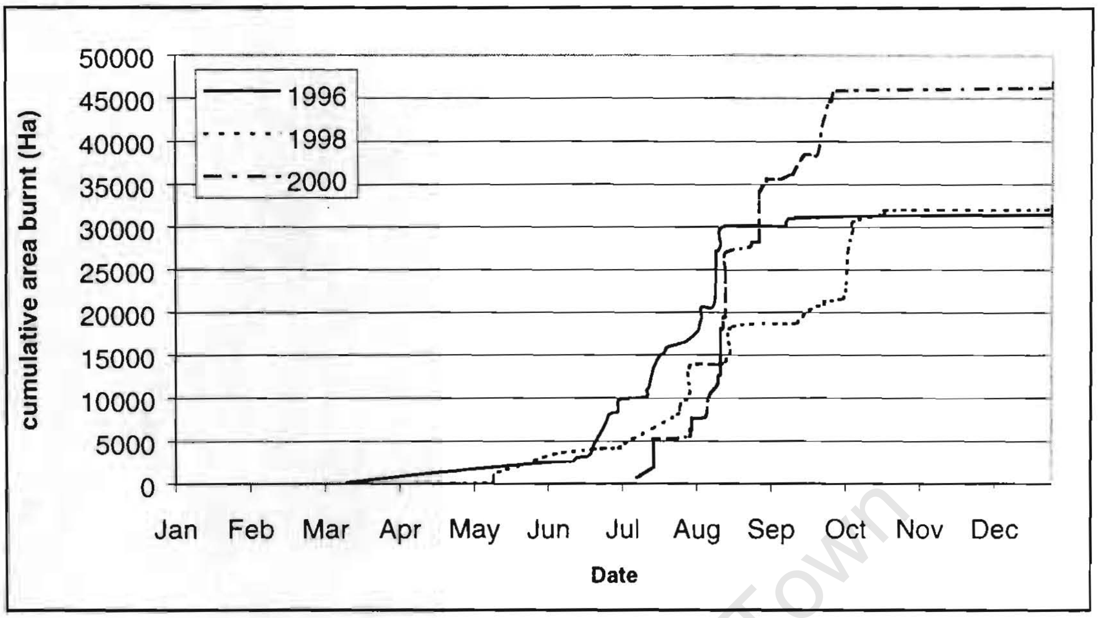

Figure 3.3: Showing how the total area burnt changed over the year for 1996, 1998, and 2000. Transect are censused from August to October.

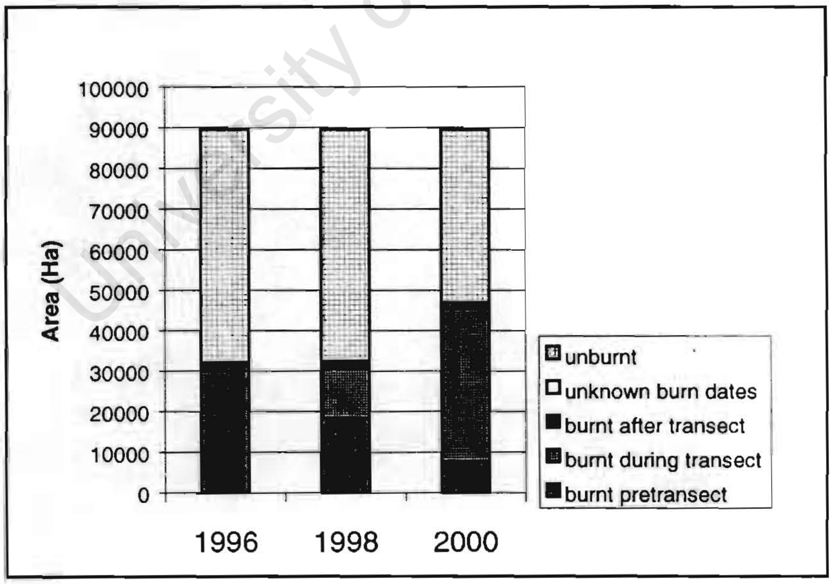

Figure 3.4: Showing differences in fire regimes between years.

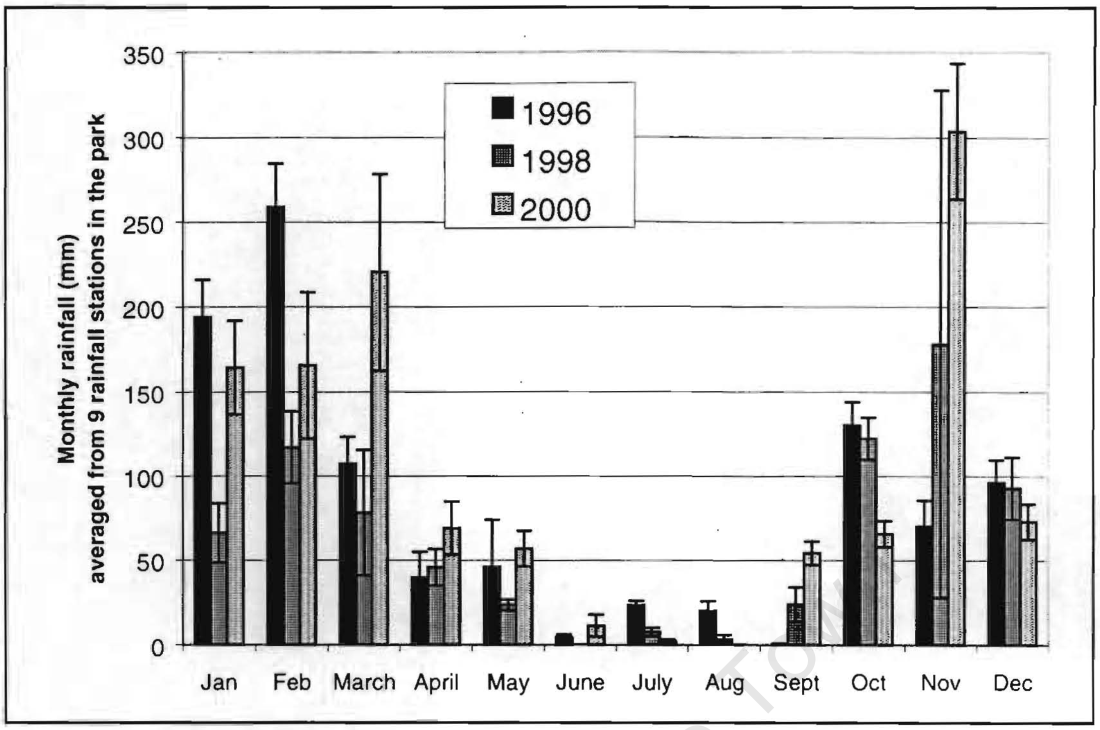

Figure 3.5: Average monthly rainfall over the whole park for each of the sampling years. Transects are censused from August to October

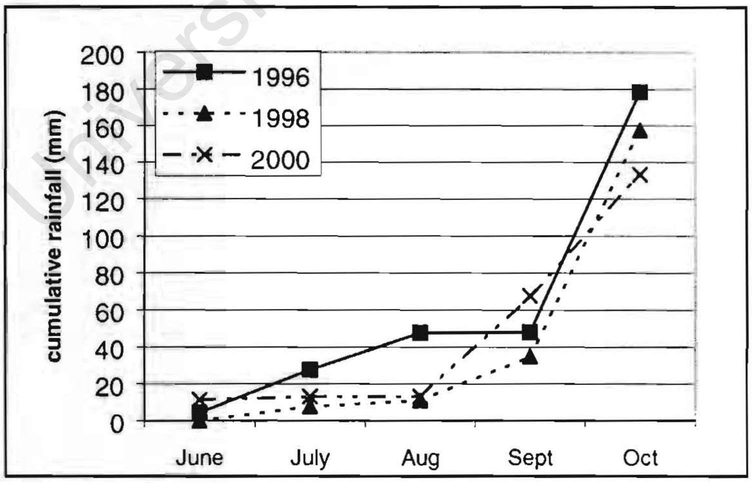

Figure 3.6: Showing cumulative rainfall until the end of the game count walks for each sampling year.

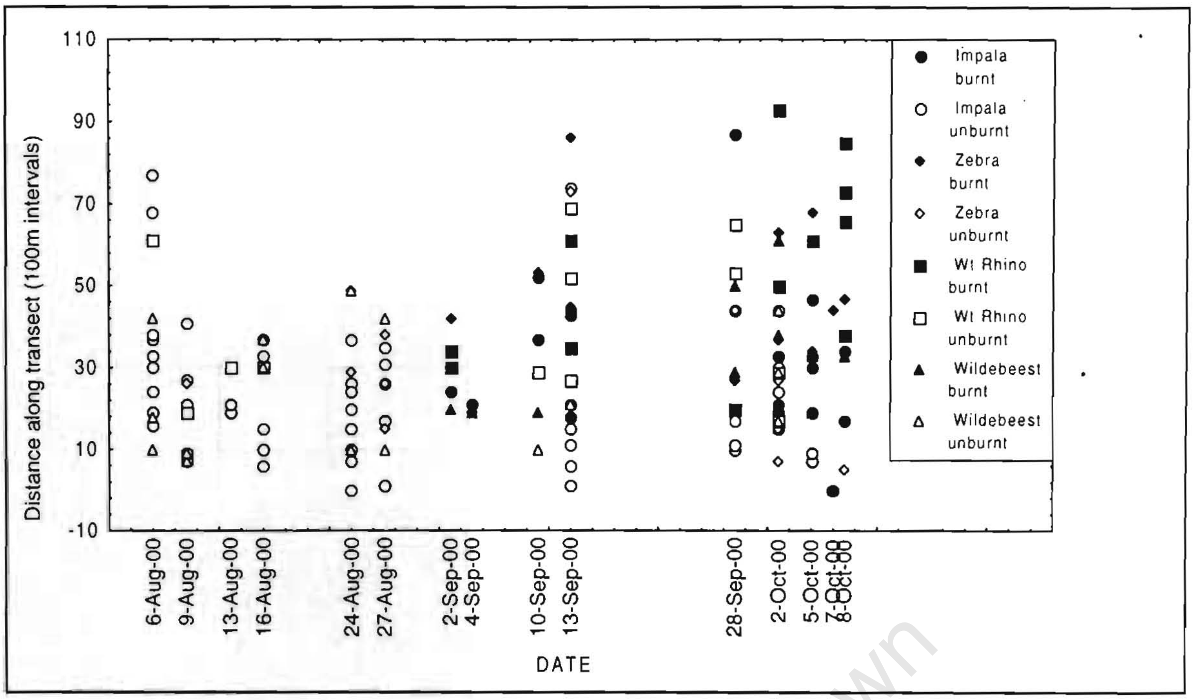

Figure 3.7: *Showing distribution of animal species along Transect 11 over time. Solid points represent a sighting in a burn, open points, in unburnt vegetation. Transect 11 was burnt on the 31 August in 2000, approximately halfway through the census period.*

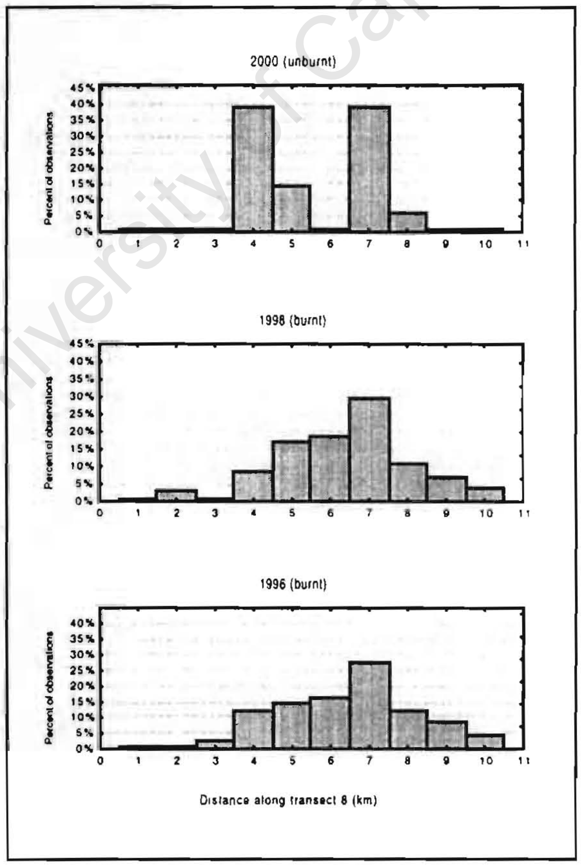

Figure 3.8: Frequency distributions of the percentage of the total animal sightings in 1km segments along Transect 8 in years when it burnt (1996 and 1998) and didn't burn (2000). When unburnt there are more sightings in fewer sections of the transect (a more clumped distribution).

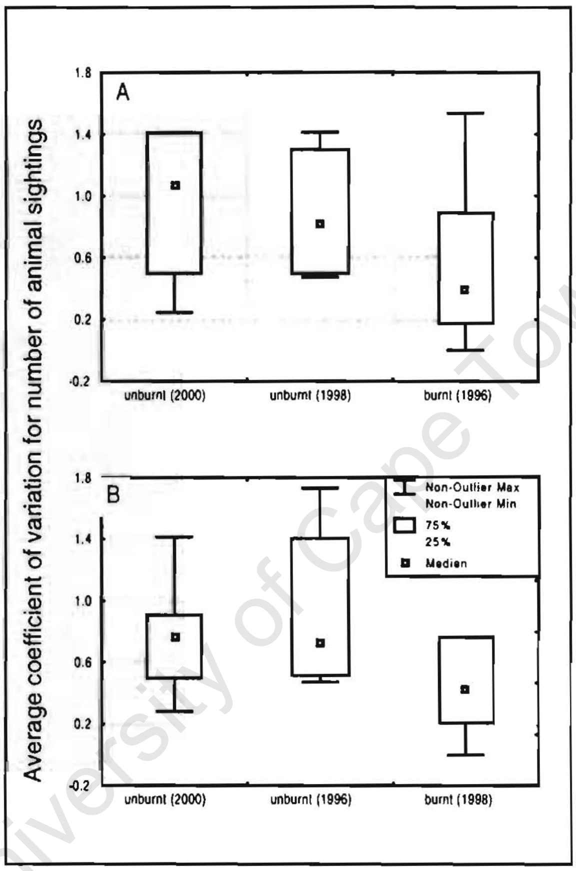

***Figure 3.9**: showing how CV of animal sightings for the same area changes depending on whether it was burnt or not. Graph A shows results for areas burnt in 1996 and not in 1998 and 2000, graph B, areas burnt in 1998, and not in 1996 and 2000 (burnt year always shown last). Generally an area had a smaller CV in years when it was burnt than in years when it was unburnt, implying that animals are more dispersed along the transects under these conditions.*

Discussion

Whether they are due to planned burns, lightning fires, or arson, large landscape-level fires are a prominent feature of most savanna and grassland systems at the end of the dry season. Before the fires animals are at their most nutritionally stressed (Owen-Smith in Scholes & Walker 1993), barely surviving on the available forage. The sudden change that fires bring about in the feeding resource is likely to alter the intensity and spatial distribution of grazing in both unburnt and newly burnt areas. I predicted that the unburnt areas would be depleted of grazing animals as the fire season progressed, and that grazing in the burnt areas would be more homogeneous, because the landscape is more uniform.

In HUP, as has also been demonstrated in other grazing systems, animals are attracted to post-fire regrowth, and more grazers are found in the burnt areas than would be expected from their proportions in the landscape (Table 3.3). This means that, conversely, fewer animals are found in unburnt areas.

Unburnt areas

The question then arises, how much does the timing and size of burn affect this process? Given that in most grassland and savanna systems something between 30 and 90% of the system can burn in a year, does the amount of area burnt have an impact on how many animals are left in the unburnt areas? Secondly, what is the timing of this process – is it more closely related to the timing of fires or the timing of the first rains?

The data indicates that the size of the area burnt does affect the density of animals in the unburnt areas (Table 3.4): there were more animals in the unburnt area in 1998 (when less of the park had burnt), than in 1996 or 2000 when almost twice as much of the park had burnt (Figure 3.2). Thus even when 20% (18 000Ha) of the park consists of palatable post-fire growth it appears that the number of animals that can make use of this resource is still limited, and will increase if the area burnt increases. This is understandable because there is a reduction in the quantity of forage available after burns (van de Vijver 1999).

Grazers also appear to be highly sensitive to timing of burning. In the year 2000, 36% of the unburnt transects showed a significant reduction in animal sightings over the sampling period (5 August – 9 October), and all transects showed a reduction in numbers (Table 3.5). That year only 7 600 Ha had burnt at the beginning of the game counts but by the end 45 000 Ha had burnt. Thus animals seem to be responding very quickly to the increase in area burnt. Rain started quite late in 2000 (only 67mm by the end of September), and the very rapid response seen here to the burns suggests that the movement is controlled more by fire than by rainfall. Many bunch grass species will flush (initiate new growth) after being burned or clipped even when there has been no rainfall (Everson & Everson 1987), although the amount of growth *is* dependent on soil moisture content (van de Vijver 1999). These newly-burnt areas can sometimes be the only source of new growth at this time of year.

In 1996 – when 94% of the burns had already occurred before the game counts – there was no clear directional change in sighting numbers on the unburnt areas. Of the transects that showed a significant change one way or the other, two increased and one decreased (Table 3.5). This also suggests that animals respond very quickly to burns, and that in 1996 grazers had already moved off the unburnt areas by the time the transects were walked (there were fewer animals overall in these areas in 1996 than their were in 1998 (Table 3.4).

Thus generally, as well as there being fewer animals in the unburnt areas than in the burnt areas, it appears that this is affected by the amount of the park that has burnt: as more of the park burns, fewer animals are found on the unburnt areas.

Burnt areas

At a landscape-level fires are resulting in a significant shift of grazing from unburnt to burnt areas. Overall there are more animals in these burnt areas. Does this mean that the grass communities are being grazed more intensively? I suggested that this would not be the case; that burnt areas provide uniformly good forage everywhere but in small quantities, so there should be a much more dispersed distribution of grazers in these areas. Although at a landscape scale there is a higher density of grazers in burnt areas, at a smaller scale - the scale of a grazing patch - the grazing intensity would still be fairly low.

By looking at the distributions of grazers along Transect 8 on different years, and Transect 11 before and after it burnt, it does appear that grazers utilise an area more evenly after it has burnt (Figures 3.7 & 3.8). Zebra and Impala in particular – short grass specialists – seem to expand their distributions after fires.

A comparison of the CV of number of sightings on different segments along the transects did not produce significant results. However, the number of animals per segment of transect *was* less dispersed around the mean in the burnt year than in the two unburnt years (Figure 3.9). The data does seem to indicate that animals are less clustered in the burnt areas.

Throughout the analysis I have used animal sightings as my unit of measurement as opposed to numbers of individual animals (which would distinguish between a group of 60 impala vs. one solitary white rhino), or kilograms of animals (which would give a measure more indicative of the actual grazing pressure represented by a sighting of animals). As mentioned in the methods, this was done so as to ensure independence of all samples, which is necessary when one is looking at habitat preference (Melton 1987; Coppedge & Shaw 1998; Gureja & Owen-Smith 2002). This method is satisfactory because for this analysis I was only interested in grazer preferences, and how this affects distributions of animals in space: the effect of these preferences, which is influenced by whether one is talking about one impala or a herd of 100 buffalo, is discussed in other chapters.
However, I did perform some of the analyses (CV and chi-squared tests) using other measures, and the results were similar to those reported here.

The benefit of this data set is the fact that there are three different years of data collected under three different fire regimes. However, this is also a cause of problems because the sampling dates and replicates for each of these years are different. The comparisons that I *was* able to do between years, and within years are in keeping with my expectations.

Grazer movements in response to fire could have interesting effects on the interaction between grazing and grass communities. By providing a large, uniform area of nutritious food in fairly small quantities it causes a movement of animals off the unburnt areas, (decreasing the grazing pressure in unburnt areas), and a spreading out of grazing in the burnt areas, (dispersing animals more evenly through the landscape). Therefore at the beginning of the wet season – an important time of the year for grass growth (Scott 1959;

Tainton & Mentis 1984) – fires are probably acting to decrease the grazing pressure at any one point in space.

One can only speculate about what would be happening in the absence of fires. Without the attraction of the post fire regrowth it is likely that animals would continue grazing in the tall bunch grass communities much longer, perhaps even a few months longer, into the growing season. Also, in the absence of the homogenising influence of fires, these bunch grass areas are likely to be grazed much more patchily – with some areas being intensively and frequently utilised and other areas ungrazed (Hobbs *et al.* 1991). The long-term consequences of these fire-, and non-fire-related grazing patterns are discussed in other chapters.

Appendix 1: *The herbivores recorded during the game counts, their food preference, and whether they were included in the analysis. Data from Kingdon (1997) and Owen-Smith (1988).*

Species	Scientific name	Food	Av. Weight (kg)	Included
Buffalo	*Syncerus caffer*	grazers (tall grass)	585	yes
Bushbuck	*Tragelaphus scriptus*	browsers		no
Bushpig	*Potamochoerus larvatus*	omnivore		no
Blue Duiker		browse/fruit		no
Grey Duiker		browse/fruit		no
Red Duiker		browse/fruit		no
Elephant	*Loxodonta africana*	browse/graze	3900	no
Giraffe	*Giraffa camelopardalis*	browsers		no
Impala	*Aepyceros melampus*	grazers/mixed	48	yes
Zebra	*Equus quagga burchelli*	grazers (short and tall grass)	235	yes
Kudu (greater)	*Tragelaphus strepsiceros*	browsers	214	no
Nyala	*Tragelaphus angasi*	browsers/mixed	85	no
Common reedbuck	*Redunca arundinum*	grazers	45	yes
Mountain reedbuck	*Redunca fulvorufula*	grazers	24	yes
Black rhino	*Diceros bicornis*	browsers		no
White rhino	*Ceratotherium simum*	grazer	1900	yes
Steenbok	*Raphicerus campestris*	browsers	11	no
Warthog	*Phacochoerus africanus*	grazers/mixed	69	yes
Waterbuck	*Kobus ellipsiprymnus*	grazers	210	yes
Wildebeest (blue)	*Connochaetes taurinus*	grazers (short grass)	187	yes

Chapter 4: preface

Showing that fires alter the distributions of grazers in the landscape is one important step in my hypothesis, but it is also necessary to show how this affects the dynamics of grazed patches in the landscape. The idea is that when animals move off the unburnt areas into the burnt areas, any short patches that might have been created by grazing grow tall again. Also, in the burnt areas the grass layer is utilised more uniformly by grazers, and again the grazed patches disappear. Thus, after burns, no part of the landscape is exposed to intensive grazing and there is no potential for lawn grass to establish.

I wanted to test these ideas experimentally, by monitoring what happens to artificially created grazing patches after fires. I was also interested in knowing more about the spatial aspects of this process: over what distances fire could be attracting grazers from unburnt areas.

Chapter 4: Grazing in context: A landscape-level experiment on the effect of fire on grazing patches in a mesic savanna ecosystem

Introduction

Grazing has a big impact on vegetation. There are numerous studies investigating how grazing alters a range of ecosystem properties; affecting ANPP, soil processes, and species composition (McNaughton 1985; O'Connor 1994; Milchunas *et al.* 1995; Tainton *et al.* 1996; Olff & Ritchie 1998). The rates and extent of these changes naturally depend on the systems being studied (Milchunas & Lauenroth 1993), but clearly grazing is a strong driver of ecosystem change. However, except in the most controlled of rangeland situations, grazing is never uniform in the landscape. Patches of more intensively grazed grass naturally develop and are preferentially utilised by grazers (McNaughton 1984; Drent & van der Wal 1999; Laca 2000; Adler *et al.* 2001). Thus the system changes mentioned above do not occur uniformly over the landscape, and they are contingent upon repeated, intensive grazing being localised in space.

A key question in these situations is therefore how long grazed patches persist in the landscape? On a landscape scale, and over a time period of years, is there any consistency in the choice of grazing patches by grazers? What factors could affect this?

These questions have never been clearly answered. While it is easy to detect and describe patterns of patchy grazing in a landscape (Pastor *et al.* 1988; Pearson *et al.* 1995; Drent & van der Wal 1999; Adler *et al.* 2001); and while it is possible to investigate processes which cause these patterns at a local level (Day & Detling 1990; Hobbs *et al.* 1991), it is harder to demonstrate how these processes are acting at a landscape level to create the patterns that we see in grazing systems.

I investigated the dynamics of grazing patches at Hluhluwe Umfolozi Park (HUP), KwaZulu Natal, South Africa. Much of this park consists of tall bunch grassland. The dominant grasses are fairly unpalatable and un-nutritious when tall, but are utilised by grazing animals when more palatable grasses are unavailable. When they are short, these bunch grasses are more palatable, and have a higher forage mass per unit volume

(McNaughton 1985), so grazing patches naturally develop in the landscape, being re-grazed and kept short by the animals. Thus it is a typical example of a grazing system where grazing creates heterogeneity (Adler *et al.* 2001). However, this is also a very dynamic system. Grass production varies because of inter-annual and inter-seasonal variation in rainfall, and large fires burn parts of the landscape every year at the end of the dry season. Over the space of a few months, or a few years, areas that were heavily grazed can be released from grazing pressure and grow up tall again, or alternatively a grazing patch can develop, with a high abundance and diversity of grazer species congregating in a previously un-utilised area. Thus it is an ideal environment to explore processes that lead to the creation and disappearance of grazed patches. Specifically at HUP my hypothesis was that the frequent large fires are important agents affecting the creation and persistence of grazed patches in the landscape.

Fire has a homogenising effect on the landscape; removing all above-ground litter and creating a uniform area of new re-growth where before there could have been a very heterogeneous vegetation structure, with grazed and ungrazed patches (Hobbs 1991, Briggs *et al.* 1998). Also (as mentioned in Chapter 3), large fires can strongly alter grazing patterns, drawing animals off unburnt areas and onto newly-growing grass in the burnt areas. Thus the effect of fire should be seen in general terms as temporarily altering the distribution and proportions of palatable grass in the landscape and thus affecting grazing.

There has been a certain amount of recognition of the interactive effects of fire and grazing on grass communities in recent years (Coppock & Detling 1986; Hobbs *et al.* 1991; Vinton *et al.* 1993). However, most of the literature has either focused on how fire affects grazer movements – without linking this to the grass layer – (Pearson *et al.* 1995; Wilsey 1996; Nellis & Briggs 1997; Coppedge & Shaw 1998; Tomor & Owen-Smith unpublished) or on how foraging patterns affect, and are affected by, structural and compositional heterogeneity – without specifying the processes/agents involved (Burns *et al.* 1988; Day & Detling 1990; Hobbs 1996; Nellis & Briggs 1997; Brock & Owensby 2000). A clear understanding of how these two factors are operating together in the landscape is yet to come. This is probably because, as Lima & Zollner (1996) point out, the scale at which people investigate grazer movements and the scale at which people understand the interaction between grazers and grass communities are very different, so it is difficult to combine the two bodies of knowledge.

I set up an experiment to test ideas about the effect of fire on grazing patches at HUP. Because it is central to my hypothesis that the dynamics of grazed patches can only be understood in the context of the surrounding landscape, it had to be investigated at a landscape level. Haddad (1999) and Haddad & Baum (1999), in investigating the effectiveness of biological corridors, have demonstrated that experiments at this scale can give results which shed meaningful answers to ecological questions where distance and spatial context are important.

Grazing patches may exist for a variety of reasons, which would lead to different degrees of permanence. For example, sodic soils may support distinctive grasslands which are heavily utilised and relatively permanent landscape patches (Scholes & Walker 1993). Because I wished to study dynamic effects of grazing patch formation and persistence, I did not use existing patches but attempted to create patches by concentrating grazers. I did this by mowing circular areas of tall grass to levels likely to attract grazers and compared animal utilisation of the mown patches against adjacent controls.

Large differences between the mown and control treatments after a growing season would indicate a persistent grazing patch. The recovery of mown treatments to control levels of grass biomass would indicate the death of a grazing patch. I was interested in the varying fates of a grazing patch depending on the proximity of burnt grasslands, which would act as a magnet, drawing grazing animals off the patches (Figure 4.1).

I was unable to test what would happen under a no-fire situation, because a large percentage of HUP is burnt every year; nor could I test how rainfall interacts with fire to affect grass growth (and thus persistence of short grass patches), because I only have data for one rainfall year. These will be explored in a simulation model in chapter 7.

The mechanisms that determine grazer foraging patterns are probably very complicated, involving interactions between biotic, abiotic, behavioural and mechanical processes at a number of different spatial and temporal scales (Senft *et al.* 1987, Laca 2000; Coughenour 1991; Bailey *et al.* 1996). However, if it can be shown how one factor – fire – is affecting the patterns of grazing in the landscape, it will not only increase awareness of the importance of fire in grazing systems, but will also be a start towards a more process-based understanding of the dynamic patterns that we see in these systems.

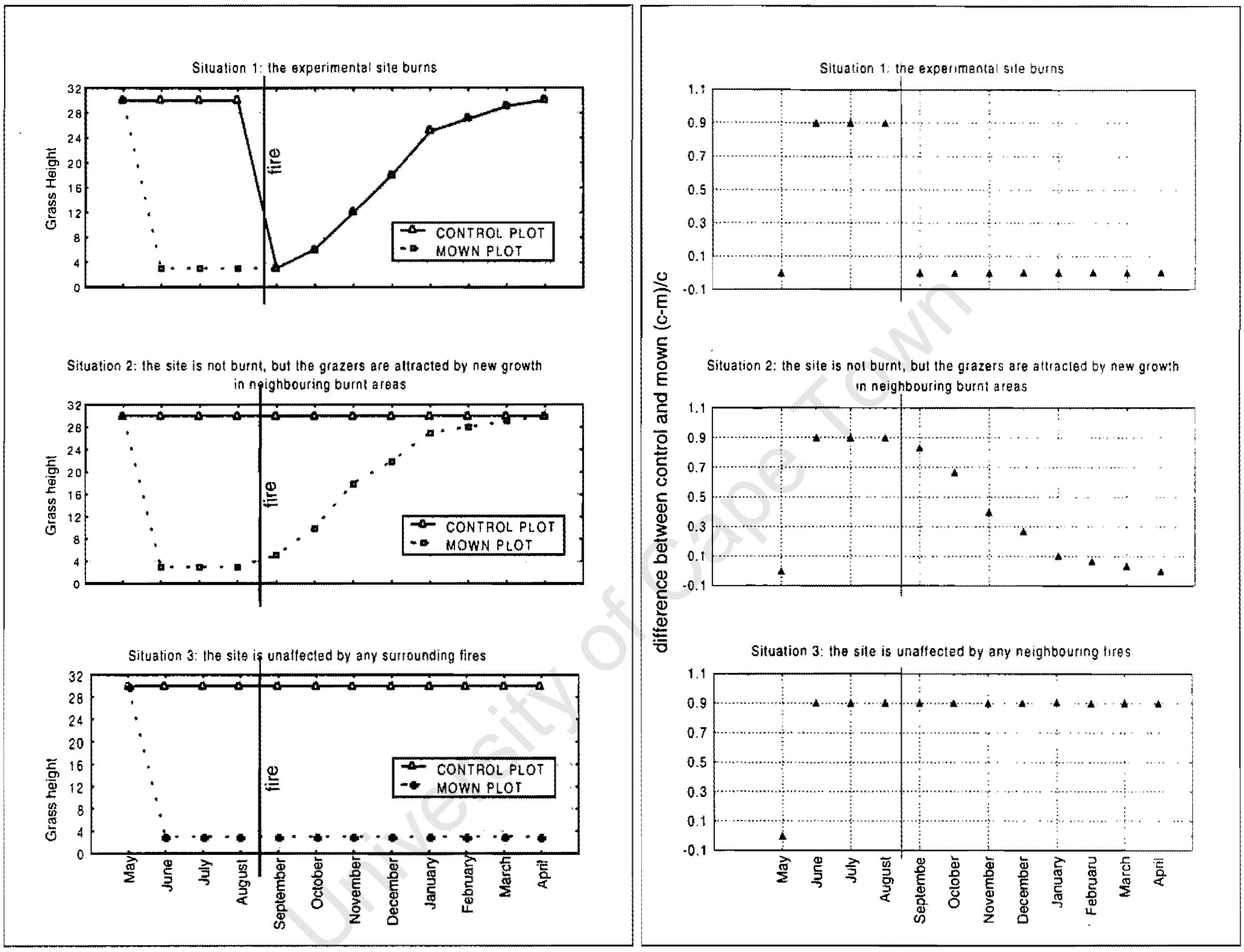

***Figure 4.1**: Expected patterns of grass height on the mown and control plots over the season: three different scenarios are possible depending on where the site is in relation to fire. Grass on the mown patch should remain short and grazed all season only if the site is far enough from a burn for its grazers to be unaffected by the post-fire regrowth.*

Methods

Experimental design

In order to test the effect of fire on the persistence of grazed patches, I first had to create a grazed patch in the landscape. My assumption was that animals are attracted to short bunch grass, and that mowing any tall grass area would create a grazing patch. However, it is likely that a range of factors, such as soil type, topography, grass community, amount of tree cover, or distance to water, could affect whether animals graze an area (Pearson *et al.* 1995; Bailey *et al.* 1996, refer to chapter 6). I wanted to find out whether short grass was enough of an attraction in itself.

I attempted to create "grazing patches" at a number of sites in a randomised block design: each site had a treatment plot (mown) and a control (unmown) plot. Thus treatment was the main predictor, with grass community and altitude (which varied between sites) being included as blocking variables (Neter 1996).

Then I wanted to know how the distribution and timing of fires affected the grazing on these patches. Thus the treatment now became burnt/unburnt with each site as a replicate in the landscape. There are some difficulties involved in setting up a landscape-level experiment. One has to compromise on intensity and resolution of sampling if one is wanting to investigate processes at this scale. At the same time, the amount of variation between sample sites at a landscape scale is very large. This invariably results in a lot of experimental error associated with the variance in ε (Neter 1996). A further problem with setting up this experiment was that it was not possible to predict or plan the treatment (burnt/unburnt) to any large degree. Managers have their own agenda when setting fires in the park, and arson fires, and fires spreading from outside the park, are frequent. There was a certain amount of discussion with managers, but ultimately which sites burnt was not under my control.

Choosing experimental sites

I had the capacity to set up 17 different experimental sites. These were chosen in consultation with the managers, to try to arrange that about half of them would burn, and that at least some of them would be as far from any burnt areas as possible. However, given that about 60% of the park is burnt each year, no area is ever more than a few kilometres away from a burnt area. Some areas in the park have many more grazing animals than others, and there is a range of altitudes, soils, and bunch grass community types in the park (see Chapter 2- site description).

I did not try to choose sites that were similar, because the variability is a characteristic of the landscape-scale at which I am investigating the process. However, nor was I able to control for this variability statistically by selecting more sites because of limited time and resources. However, this experimental design does give an indication of how important fire is against the background noise of other environmental variables, and, most importantly, over what distances it might be operating in the landscape.

I chose 17 sites that were broadly representative of the range of tall bunch grassland communities present in Hluhluwe. The sites were scattered throughout the northern section of the park (Figure 4.2), and ranged from 100m to 460m above sea level, and from 28.24° S, 31.95° E to 28.04° S, 32.13° E. They represented a variety of different bunch grassland communities which I classified into 4 broad categories: *Themeda* grassland, *Sporobolus* grassland, mixed chlorodoid grassland (*Digitaria eriantha, Eragrostis curvula, Trystachya leucothrix)*, and mixed andropogonoid grassland (*Cymbopogon excavatus, Hyparrhenia filipendula).* I tried to keep slope and tree cover constant. Most of the sites were on soils derived from sandstone or shales and had experienced a median fire return interval of about 4 years for the last 40 years (Table 4.1).

Because there was a mown and an unmown plot at each site I was able to control for variation between sites by calculating the difference between the mown plot and the control plot. This is a measure of the persistence of the grazing patch: once there is no longer a difference between the mown and control plots then the grazing patch has disappeared. This way the initial differences in grass height, grass species, grazer species, and grazing intensity between sites are less apparent but I am still asking the basic question: "how does fire affect whether a short grazed patch persists in a bunch grass landscape?"

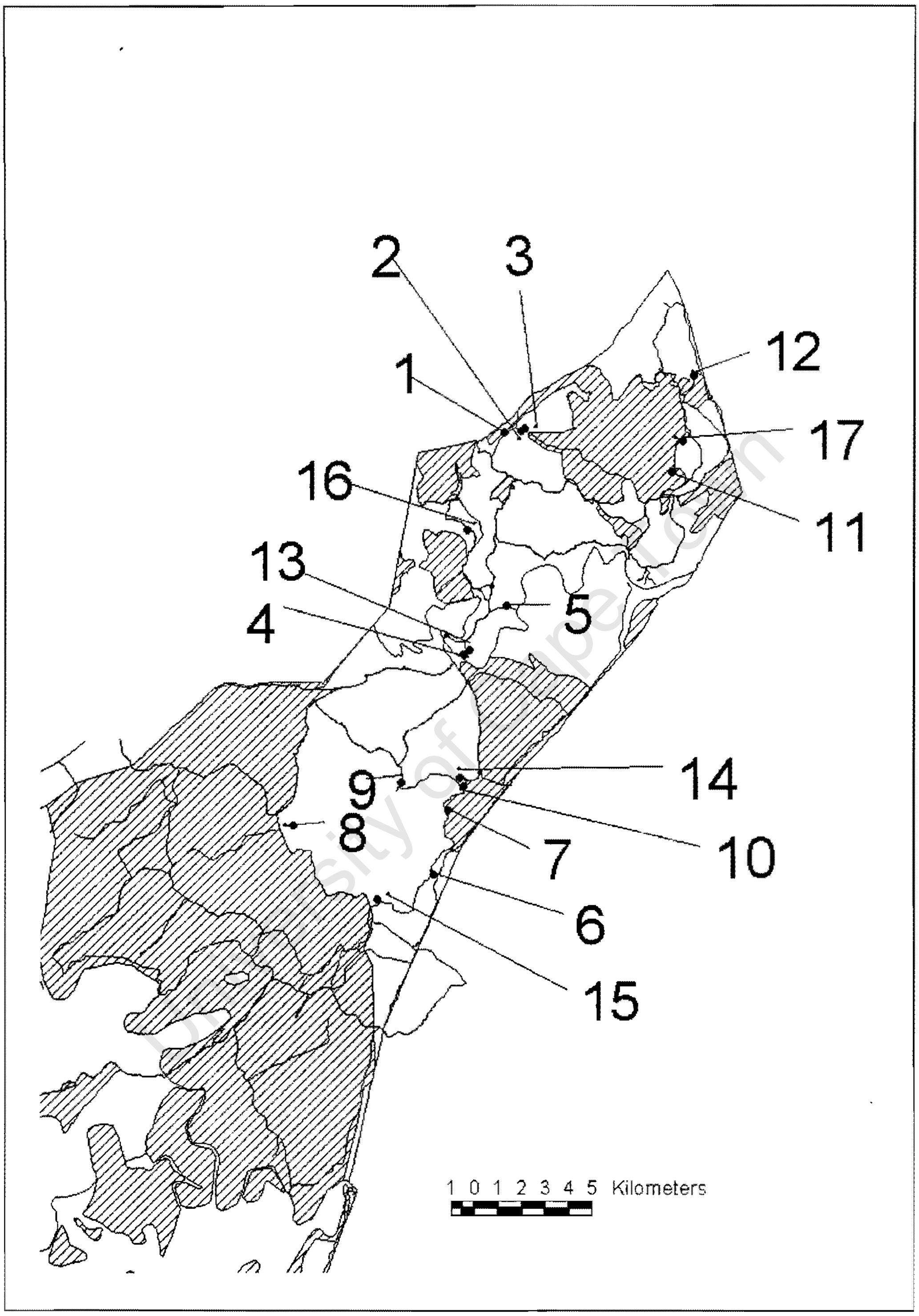

Figure 4.2: *Location of the 17 experimental sites at Hluhluwe Game Reserve. Shaded areas are areas that burnt during 2001.*

Table 4.1: Information about the 17 experimental sites

site number	Latitude	Longitude	grass community type	Altitude	Geology	Number of fires in the last 40 years	burn status 2001	distance from closest burn (m)
1	-28.0620	32.0456	Mixed andropogonoid	439	sandstones, shale	3	near burn (<300m)	60
2	-28.0622	32.0527	Mixed andropogonoid	464	sandstones, shale	11	near burn (<300m)	250
3	-28.0616	32.0559	Mixed andropogonoid	406	sandstones, shale	13	Burnt	0
4	-28.1477	32.0294	Sporobolus (chlorodoid)	100	shales, thin sandstones	11	far from burn (>1300m)	1300
5	-28.1286	32.0469	Sporobolus (chlorodoid)	160	sandstones, shale	11	far from burn (>1300m)	1480
6	-28.2316	32.0165	Mixed andropogonoid	258	sandstones, shale	15	intermediate	1260
7	-28.2060	32.0233	Mixed chlorodoid	211	sandstones, shale	10	Burnt	0
8	-28.2126	31.9569	Themeda (andropogonoid)	306	sandstones, shale	18	intermediate	630
9	-28.1962	32.0027	Themeda (andropogonoid)	288	sandstones, shale	13	far from burn (>1300m)	2050
10	-28.1979	32.0291	Sporobolus (chlorodoid)	220	sandstones, shale	12	Burnt	0
11	-28.0771	32.1183	Mixed andropogonoid	193	conglomerate sandstone shale	15	Burnt	0
12	-28.0398	32.1270	Themeda (andropogonoid)	280	conglomerate sandstone shale	16	near burn (<300m)	160
13	-28.1461	32.0309	Sporobolus (chlorodoid)	105	shales, thin sandstones	11	far from burn (>1300m)	1340
14	-28.1952	32.0278	Sporobolus (chlorodoid)	213	sandstones, shale	13	near burn (<300m)	180
15	-28.2407	31.9927	Sporobolus (chlorodoid)	161	sandstones, shale	19	intermediate	430
16	-28.0993	32.0298	Mixed andropogonoid	161	tillite breccia	18	burnt	0
17	-28.0649	32.1229	Mixed andropogonoid	198	conglomerate sandstone shale	18	intermediate	500

Sampling methods

At each site I marked out two circular plots (20m diameter), keeping the grass species, slope, and tree layer as similar as possible between plots. Initial measurements were taken on both plots, and then I randomly allocated one plot for mowing, and cut the grass on this plot to a height of <10cm. All bushes and shrubs on the plot were also cut. The grass height on the mown plot was then re-measured.

The initial mowing treatment occurred during May 2001 at the end of the wet season. This is the time when grazers are moving off the lawn grass areas and starting to utilise tall-grass areas. The way in which the animals graze in tall-grass areas is to create patches of short, grazed grass within the landscape, and the treatment was intended to create such a grazing patch artificially. Subsequently I returned to each site and took measurements once a month for one growing season. In September rain gauges were set up at each site. Very little rain had fallen in the park before then (c. 10mm), the rain only started in October. Also at this time I put up small 1 x 1m exclosures on each plot to give me data on grass growth without grazing. Measurements of the five following characteristics were taken each month:

- Grass Height of the plot (43 Disc Pasture meter readings spread evenly throughout the plot)
- Grass Height inside/outside the temporary exclosure (5 DPM readings on 4 corners and in the centre)
- Dung (Measured in a 8x20m belt transect. Two field assistants walked along the transect searching consecutive 4x2m plots for dung. When new dung was found the species and freshness (fresh, medium, old) of the dung was recorded. It was then marked with a stick so that it would not be counted again in following months. The same dung transect was walked each month.
- Amount Bitten: This was a measure of the amount of the standing grass sward that was bitten. A 20m long tape measure was run through the centre of the plot and every meter along the tape the percentage of that meter that was bitten grass sward, unbitten grass sward, and bare ground, was estimated. Any shoots that were bitten were counted as bitten, regardless of bite height. After the plots were burnt/mown it was no longer possible to differentiate between bitten shoots and burnt/mown shoots. In these cases this measure gives an indication of the amount of unbitten new growth available.

Analysis

Question 1: Does short grass attract grazers? Can you create a grazing patch by mowing?

Dung counts were used as an indication of grazer presence. This has been tested successfully in various studies (Lawes & Nanni 1993; Marques *et al.* 2001), and is being calibrated at HUP using field observations and video cameras. There are certain problems with using dung at HUP. White rhino, a prominent grazer in the system, dung in middens. Different species dung differently and also have different body weights, so differences in dung quantity do not reflect differences in the amount grazed. Buffalo don't generally dung while they are grazing, but after they have been sleeping (Jolles pers comm.).

I investigated various methods for looking at grazer presence: simply using total dung; using a dung index which combined a measure of grazer diversity with grazer presence; using a very simple dung index that just recorded presence, a few, and a lot of dung; and separating dung into tall grass and short grass grazer species. The best results seemed to come from using the raw data on dung count, i.e. the number of separate dung piles found at each site each month.

To investigate how other factors besides the treatment contribute to the variation in grazer presence that was found between sites, I ran a multi-factorial ANCOVA. My dependent variable was dung count (logged), and predictor variables were Treatment (2 factors), Grass community (4 factors), and Altitude (continuous). I ran separate analyses for three months: one for May 2001 (before the mowing treatment), and one each for June and July 2001 (after the mowing treatment but before the fires).

Question 2: How is the persistence of a grazed patch affected by its proximity to a burnt area?

After the burns, using ARCVIEW GIS software I calculated the distance of each site from the closest burn. Five sites had burned, and the others ranged from 60m from a burn to 2050m. For the purposes of analysis I divided the sites into 4 approximately equal categories: 5 burnt sites, 4 sites near a burn (within 300m), 4 intermediate, and 4 far from a burn (>1300m from a burn) (Table 4.1). This allowed me to test the expectations set up in Figure 4.1: if the grazing patch was still present at the end of the experiment then the grass height on the patch would still be different from pre-treatment height. I performed a

Mann-Whitney U test between grass height data in May 2001 (pre-treatment) and April 2002 for each of the four distance categories.

Results

During the fire season 5 of the sites burnt, 4 were within 300m of a burn, and the other 8 ranged from 430m to 2050m from a burn (Table 4.1). Generally the sites that burnt were mixed andropogonoid, and the sites very far from a burn were *Themeda* andropogonoid, but there were representatives of most grassland types in each burn category.

Question 1: Are grazers attracted by short grass patches in the landscape?

Figure 4.3 shows how the average amount of dung changed on the mown and control plots after the plots were mown. Before the plots were mown (May) there was no difference between the plots. After they were mown there was a highly significant increase in the amount of dung found on the mown plots. However, all grazer species did not respond to a similar degree. Figure 4.4 shows that impala, nyala, wildebeest and warthog responded to the mown treatment much more often than zebra or buffalo. Using this information I classified the grazers into short-grass species (impala, nyala, wildebeest and warthog) and more generalist/long grass species (zebra and buffalo). Figure 4.5 shows how after the mowing treatment both the amount of dung, and the amount of dung from short grass species increases dramatically. However, Figure 4.5 also shows that initially, and after the mowing treatment, there is a great deal of variation between the various sites.

An ANCOVA explored the causes of this variation, and tested whether factors other than the height of the grass affect whether a grazing patch develops (Table 4.2).

Before the mowing treatment altitude was the only factor which significantly affected grazer presence, but the treatment over-shadowed this pattern: after the sites were mown the factors that significantly predicted grazer presence were treatment (control/mown) and, in June, the interaction of treatment*grass community. Because the sample size is very small it is possible that this analysis was open to type 1 or type 2 error. To test for this I did a sensitivity analysis, randomly excluding 1 and then 2 samples from the analysis to see whether it altered the results in any way. I did this five times for each month. The results were robust, although sometimes there was no treatment*community interaction.

Table 4.2: Results of ANCOVA on the amount of dung found at the experimental sites (indication of grazer presence)

		May: before treatment		June: 1month after treatment		July: 2 months after treatment	
summary of effects	degrees of freedom	Wald statistic	P	Wald statistic	p	Wald statistic	p
Intercept	1	3.51	0.06	**14.42**	**0.00**	**4.13**	**0.04**
Altitude	1	**6.65**	**0.01**	0.25	0.62	2.18	0.14
Treatment	1	0.07	0.80	**15.23**	**0.00**	**7.02**	**0.01**
Grass community	3	4.50	0.21	1.67	0.64	2.67	0.45
Treatment*community	3	2.09	0.55	**8.20**	**0.04**	3.83	0.28
goodness of fit	Degrees of freedom	Stat.	Stat/Df	Stat.	Stat/Df	Stat.	Stat/Df
Deviance	25	21.53	0.86	19.58	0.78	29.03	1.16
Scaled Deviance	25	34	1.36	34	1.36	34	1.36
Pearson Chi²	25	21.53	0.86	19.58	0.78	29.03	1.16
Scaled P. Chi²	25	34	1.36	34	1.36	34	1.36
Loglikelihood		**-40.48**		**-38.86**		**-45.56**	

Table 4.3: Summary statistics for the ANCOVA of log(dung count) for June 2001

Factor	*Level of factor*		*n*	*Mean*	*St.Dev.*	*Cnf.Lmt -95*	*Cnf.Lmt +95*
Total			34	2.09	1.09	1.71	2.47
Treatment	mown		17	2.68	1.13	2.10	3.26
Treatment	control		17	1.51	0.69	1.16	1.86
Grass community	Mixed andropogonoid		14	2.13	1.09	1.50	2.75
Grass community	Sporobolus		10	2.16	1.25	1.27	3.06
Grass community	Mixed chlorodoid		4	2.40	1.49	0.03	4.77
Grass community	Themeda		6	1.70	0.63	1.04	2.36
Treatment*grass community	mown	Mixed andropogonoid	7	2.25	1.50	0.86	3.64
Treatment*grass community	mown	Sporobolus	5	3.19	0.57	2.49	3.89
Treatment*grass community	mown	Mixed chlorodoid	2	3.65	0.13	2.49	4.80
Treatment*grass community	mown	Themeda	3	2.16	0.33	1.35	2.97
Treatment*grass community	control	Mixed andropogonoid	7	2.00	0.51	1.53	2.47
Treatment*grass community	control	Sporobolus	5	1.13	0.75	0.20	2.06
Treatment*grass community	control	Mixed chlorodoid	2	1.15	0.65	-4.67	6.97
Treatment*grass community	control	Themeda	3	1.23	0.48	0.04	2.42

Table 4.3 gives summary statistics for the blocked design. In June, there was an interaction between treatment and grass community. This indicated that the grazer response to the treatment was much stronger on the *Sporobolus* and mixed chlorodoid plots than on the *Themeda* and andropogonoid sites. The difference between the mown and control was much less on the mixed andropogonoid and *Themeda* sites (which also happen to be the sites at higher altitudes) than on the other sites.

Figure 4.6 is a scattergram of grass height in relation to grazer presence (dung counts) using all the data available (all plots all months). There does seem to be a pattern; with more dung being found when the grass is short. The vegetation height at which grazer presence drops off is about 10-15cm.

Question 2: How did fire affect grazing on the experimentally created grazing patches?

Figure 4.7 shows grazer presence at the 17 mown sites two months before the fires, two months after the fires, and two months in the middle of the growing season. Before the fires there was random variation in the amount of dung at each site, with very large numbers of dung being found at some sites (see y axis). After the fires all the burnt sites had a very high grazer presence. There was much less dung at the sites close to burns. Several sites far away from burns still had large amounts of dung. Later in the growing season there was still high grazer activity on the burnt sites, but grazing at most other sites, especially ones very close to the previously-burnt areas, was greatly reduced.

Question 3: How did grass height change throughout the season and with distance from burnt areas?

Figure 4.8 shows average grass height on the mown plot and the control plot for four different distance categories from burnt areas. The grass stayed short (grass height significantly different from initial grass height, Mann-Whitney U $p<0.05$) on the plots that burnt and also on the plots that were furthest away from the burns. In the plots close to the burns the grass grew up again to be as tall as it was before the treatment. Thus for these plots the grazing patch that was created at the beginning of the season had disappeared by the end of the season. Effectively the grazing patch also disappeared in the areas that burnt, because in these areas the grass height, while still short, was the same on the mown plots and the control unmown plots.

Figure 4.9 shows, for each plot, the difference between the grass height at the end of the season and the grass height at the beginning of the experiment in relation to the distance from the closest burn. There is no difference for the control plots, but the further the mown plots are from a fire the more pronounced the difference still is at the end of the season.

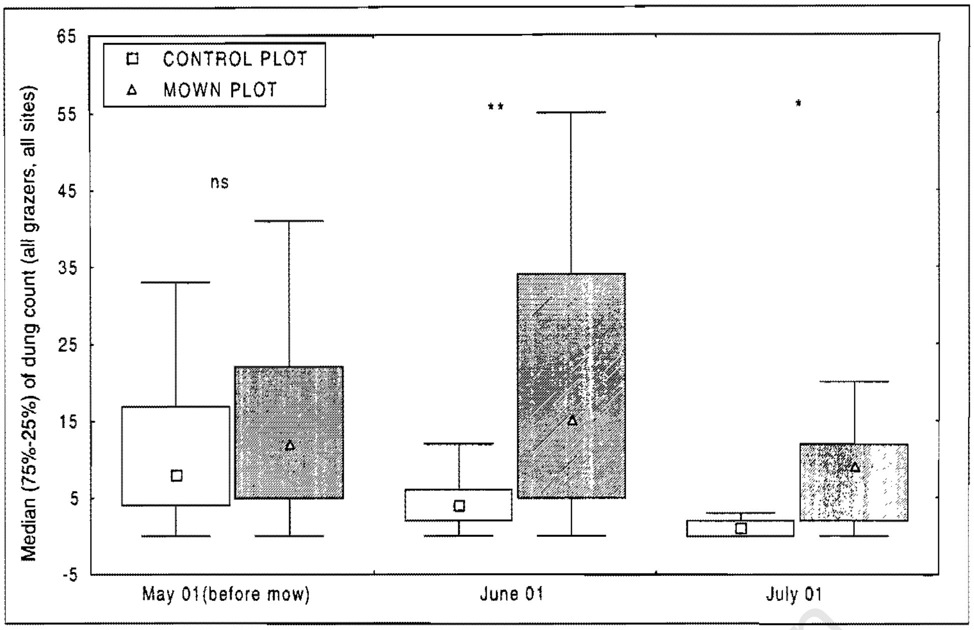

__Figure 4.3:__ Median of dung count on all sites before the sites were mown (May 01) and for two months after. Significant differences between control and mown plots are indicated (Wilcoxons signed ranks test, n=17, p=0.031, 0.002 and 0.012 respectively):

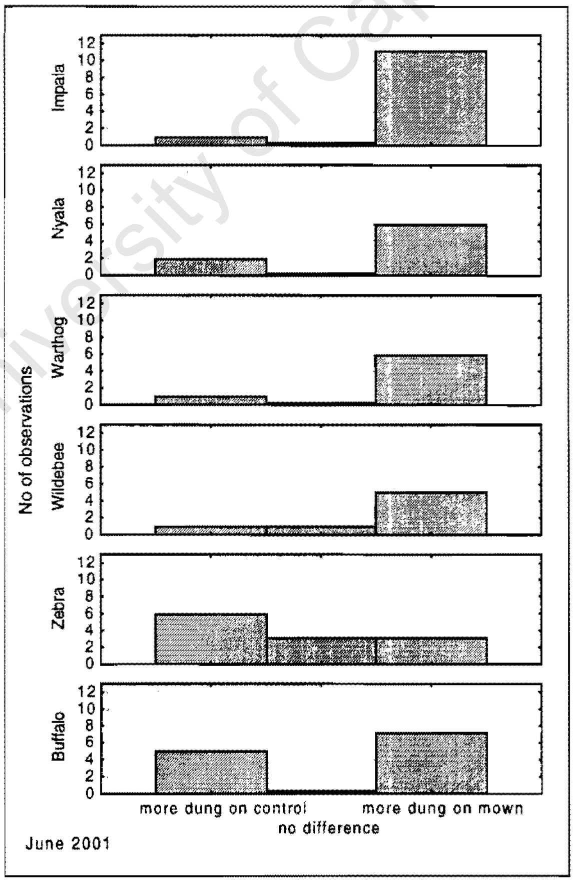

__Figure 4.4:__ Indicating the responses of different grazer species to the mown plots. Data shown is for June 2001, the first month after the sites were mown. Frequency distributions represent the number of sites where more dung was found on the mown than on the control plots.

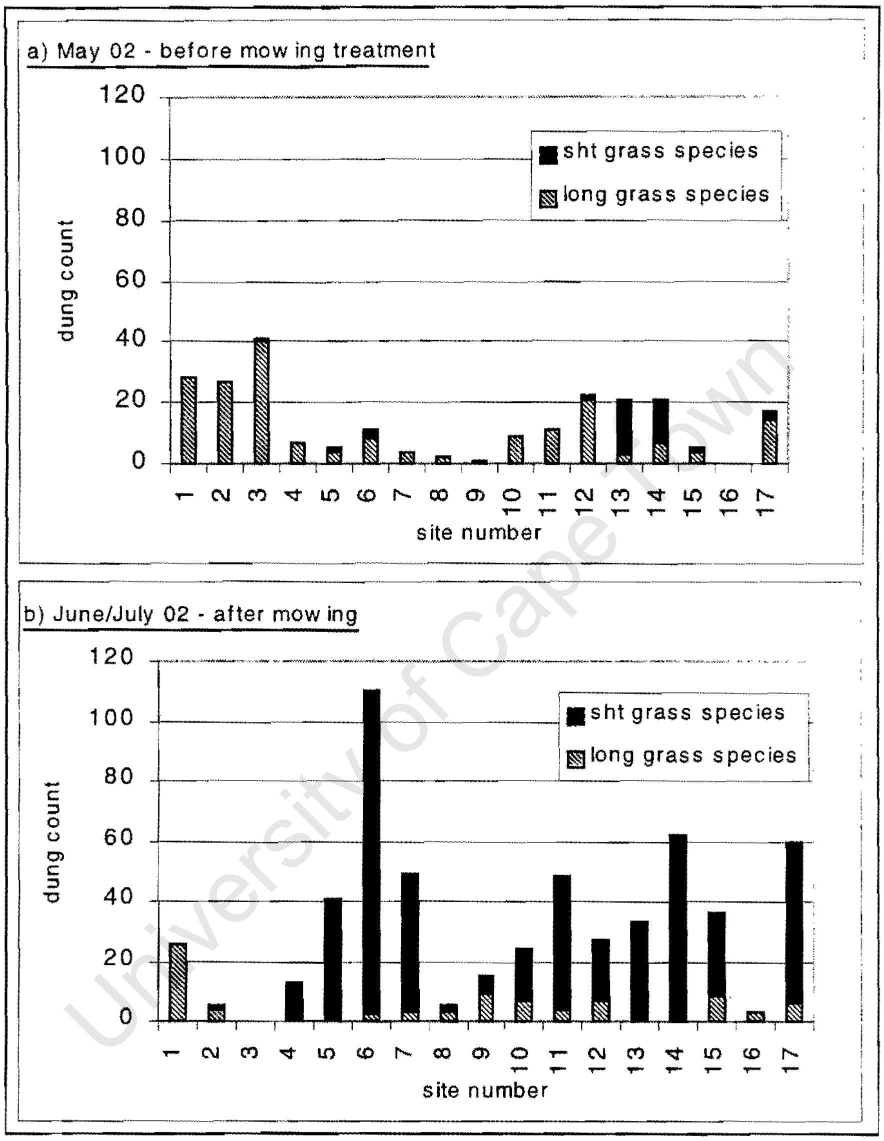

Figure 4.5: *Graph showing total dung of short and tall grass grazer species on each site (short grass grazers: impala, nyala, wildebeest, warthog. Tall grass grazers: buffalo, zebra). The treatment effect was much larger at some sites than at others. See results of ANCOVA (Table 4.2) for an investigation of the sources of this variability between sites.*

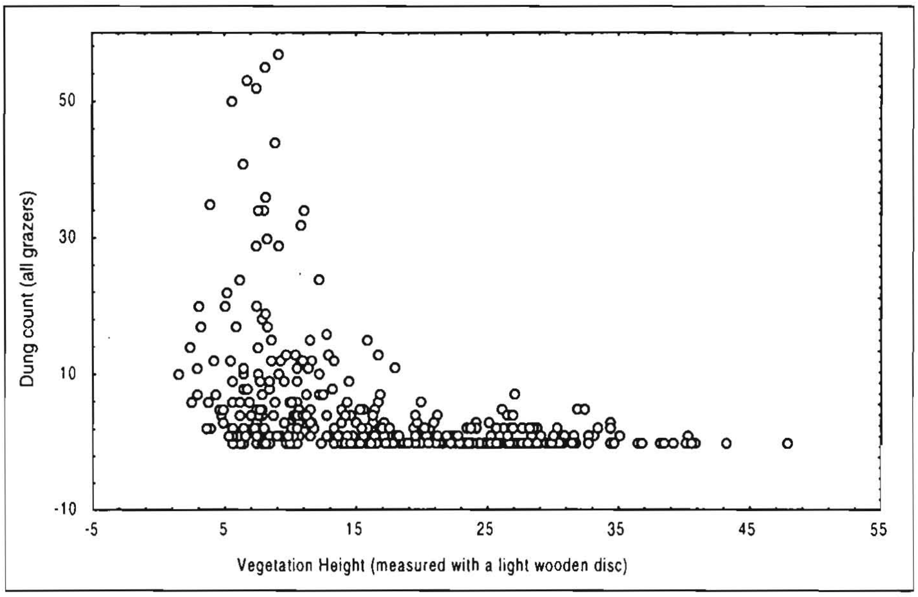

***Figure 4.6**: Scatterplot showing how dung count is related to vegetation height (as measured with a vegetation height meter): much less dung is found when the grass height becomes greater than 10-15cm tall.*

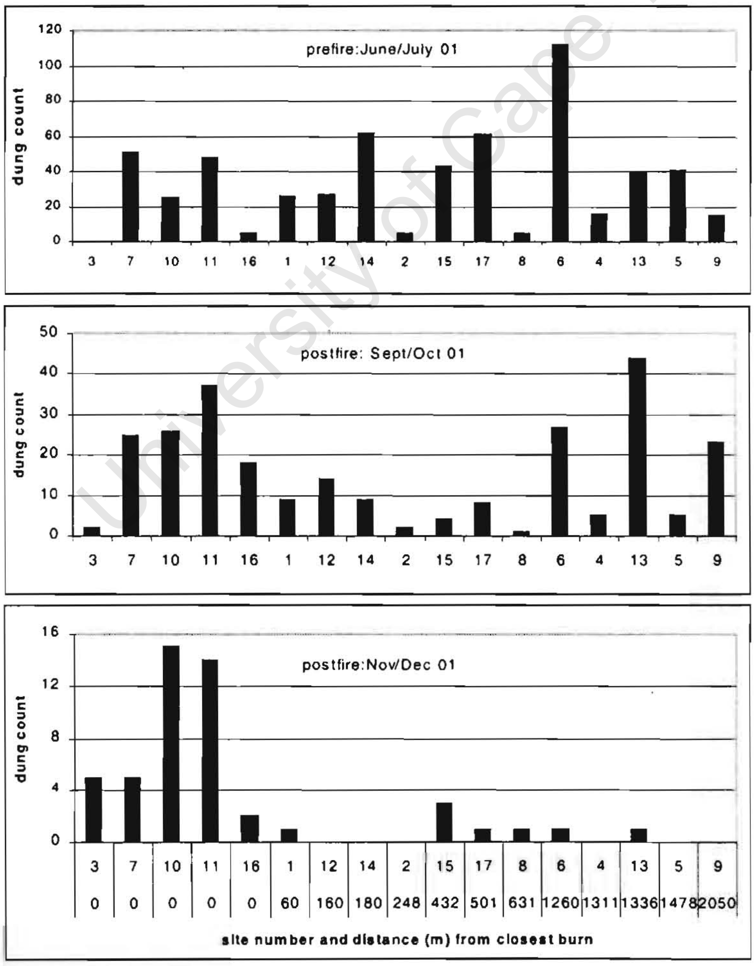

***Figure 4.7**: Showing how grazer presence varies with distance to a burn for three different time periods. Grazer presence is measured in terms of total dung counts: note the difference in the y axes on different dates.*

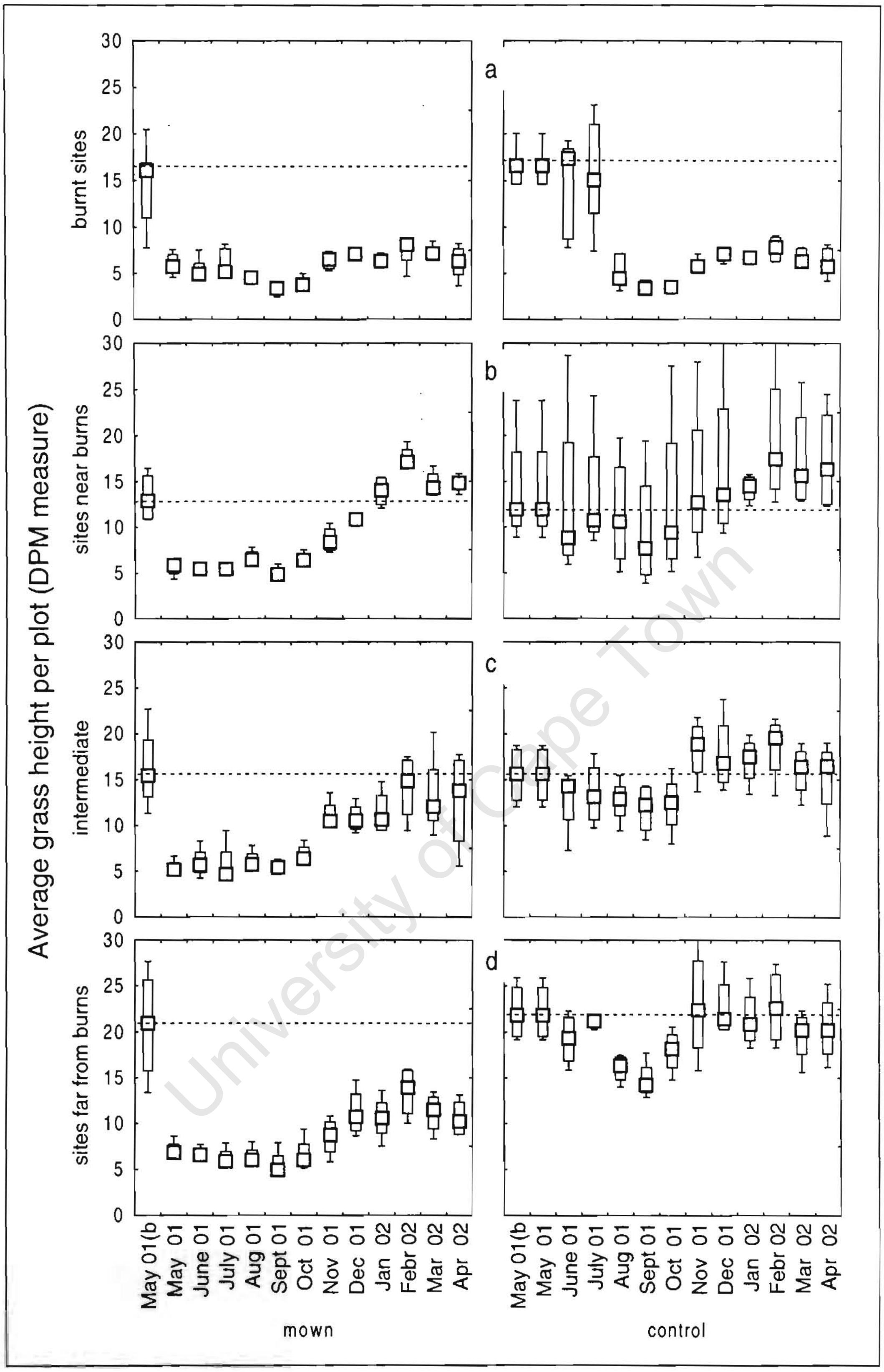

Figure 4.8: *Median grass height on the mown and control plots for four different categories of distance from burnt areas. Whether the grass at the sites grows up tall again during the season depends on its situation in relation to the fires of that year. Significant differences in grass height between May 01 and April 02 (Mann-Whitney U, $p<0.5$) were recorded on the burn plots (mown and controls) and on the mown plots far from the burns.*

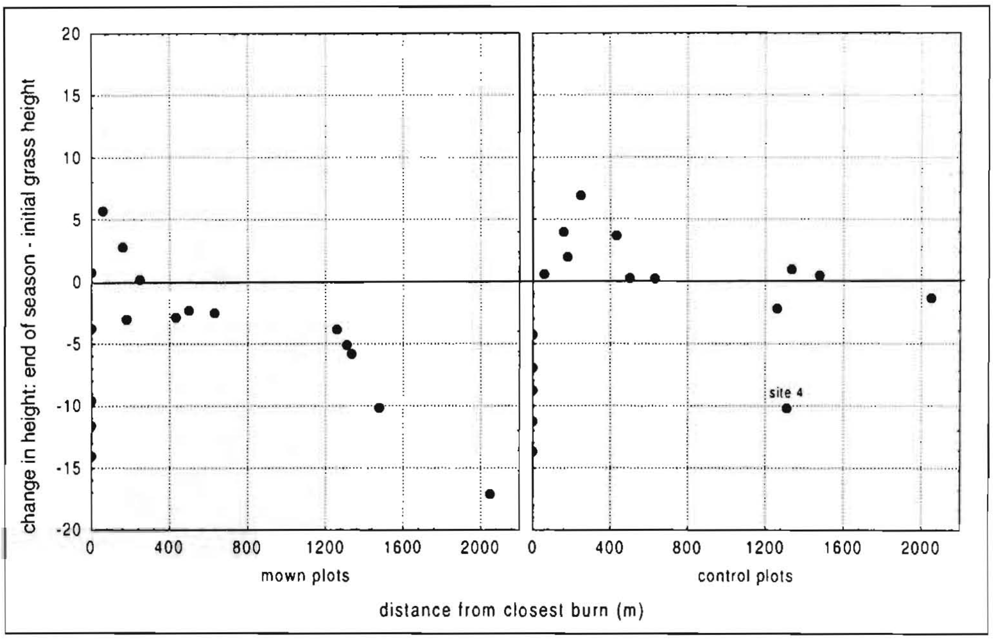

Figure 4.9: Showing ΔHt in relation to distance from a burn. A more negative value indicates that the grass is still short and that the grazing patch is still present in the landscape after one year. There was no change in grass height for the control plots (the change shown in site 4 was due to the fact that the grass got compressed at this site by buffalo resting there).

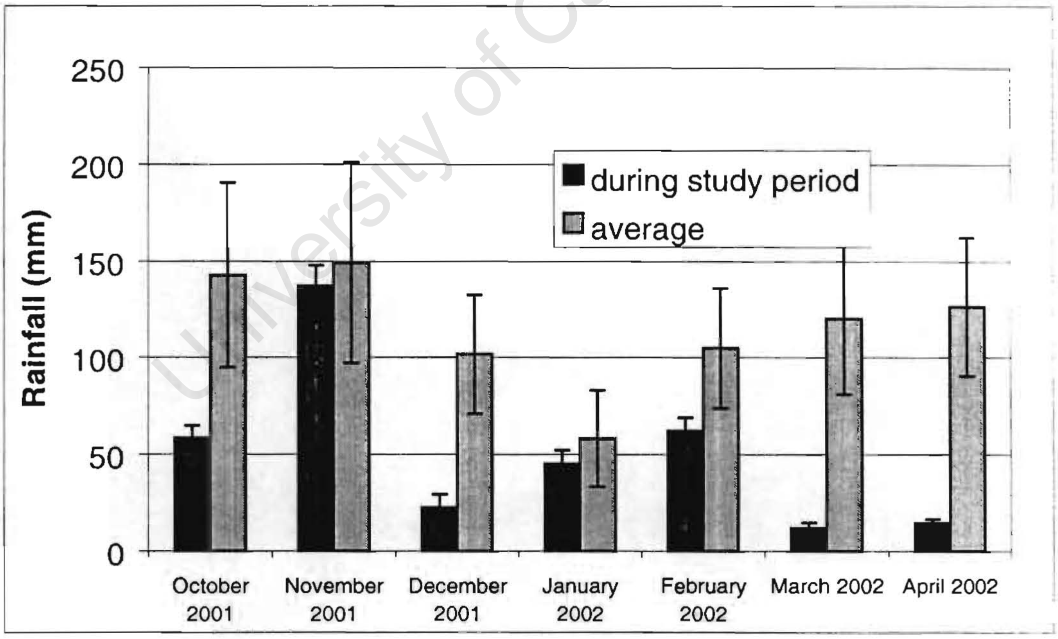

Figure 4.10: Rainfall during the study period (the average from rain gauge readings at all experimental sites) compared with the average rainfall for the park (rainfall records since 1933)

Discussion

This experiment gives some interesting insights into the interaction between fire and grazing in controlling the distribution, creation and persistence of grazing patches in the HUP landscape. It is apparent that grass height is one of the most important factors determining whether an area will become a grazing patch – over-riding other landscape factors such as altitude and variation in grass community type. This is in keeping with observations in the park – that grazed patches occur under a range of environmental conditions.

Whereas it is well demonstrated that grazed areas are generally re-grazed and become grazing patches in the landscape (McNaughton 1984; Hobbs *et al.* 1991; Catchpole 1993; Drent & van der Wal 1999), this appears to be the first test of whether short grass alone is enough of an incentive to cause animals to maintain a grazing patch. Mowing increased both animal presence and the presence of short grass grazer species in most sites (Table 4.2, Figure 4.5). While the strength of this effect is potentially mediated by the grass community present (Table 4.3), the effect did hold over a range of altitudes and community types.

This is interesting because it means that at HUP grazing patches are potentially very unstable: in many situations it is only the fact that they are grazed short, and continually re-grazed, that is causing them to persist in the landscape: the moment they grow up tall again the effect of the grazed patch disappears.

If grazed patches are only distinguished from the rest of the landscape by the height of the grass, then any temporary release of grazing pressure, or an extremely good rainfall season could cause the grasses to grow tall enough to discourage grazers so that the grazing patch would disappear. Over time, intense grazing can alter many system/community properties of an area (Milchunas & Lauenroth 1993; O'Connor 1994) and if grazing persists in a patch for a long enough period, nutrient cycling and species composition do change. At Hluhluwe Umfolozi Park it is likely that a grazed patch would have to persist in the landscape for a number of years before its grass species and soil properties became significantly different from the surrounding vegetation. Research in other tall-grass systems suggests that this is the case elsewhere also (Vinton *et al.* 1993).

When seen in this context, fire could be one of the main factors controlling the distribution and persistence of grazed patches in a landscape, by dispersing grazers. Fire, which is itself very variable between years and in space, could be causing the variability that we see in the appearance and disappearance of grazing patches in the landscape of Hluhluwe.

The data shows how, after fires, grazer presence (dung counts) increased on the burnt plots, and decreased on the unburnt plots that were near to the burns (Figure 4.7). It also showed that sites further from burns (> c. 1km) were less affected by this attraction of animals to the burnt plots. These effects were still apparent many months after the burns, giving ample time for the grass in areas released from grazing pressure to grow up tall again. Grass at sites that were close to the burns did indeed recover initial biomass by the end of the season (Figure 4.8b). The mown plots were kept short by grazers until the fires occurred, and then grass grew up very quickly over the space of about four months and regained its original height before the grazing patch was initiated.

The pattern of grass growth at these sites can with confidence be attributed to the effect of the fires, because sites further away from the burnt areas did not grow up tall again. At these sites the grass continued to be grazed short and the grass height at the end of the grazing season was still significantly different from the pre-treatment condition (Figure 4.8d). Thus the grazed patches persisted throughout the season in areas further from the fires. (Catchpole 1993) noted similar patterns with bison grazing in a tallgrass prairie system: grazed patches were re-selected 59% of the time, whereas only 35% of the patches in burnt areas were re-selected.

Sites at intermediate distances from a burn showed variable responses (Figure 4.8c). It is possible that this category is a mixed category, consisting of sites that were affected by the burns, as well as sites that weren't (this implies that the scale at which fire is affecting animal distributions is between 400 and 1300m). This pattern can be seen in the scattergram of difference in grass height at the beginning and end of the season vs. distance from a burn (Figure 4.9): the difference between the end of season grass height and the initial grass height was clearly related to how far away from the fires the mown plots had been, whereas the control sites showed no pattern with distance, and generally no difference between the start and end of the experiment.

Figure 4.6 suggests that there is a threshold grass height (10-15cm) above which bunch grass becomes much less attractive to grazers. This is corroborated by work in East Africa (Talbot & Talbot (1963) state that wildebeest prefer grass less than 4 inches). The sites that remained below 10cm at the end of the grazing season, and therefore persisted as grazing patches into the next season, were either quite far from any burns (500, 1km and 2km), or else had burnt that year.

The results for the burnt areas were contrary to expectations: I had expected that even though many animals are attracted to burnt areas, the areas are so large (37% of the park in 2001), and uniformly highly-palatable, that grazing on these areas would be diffuse and widely distributed and that the grazing pressure would not have been enough to keep the grass short (Figure 4.1). However, in 2001 the burnt areas did remain short. Thus while the grazing patch created by the mowing treatment disappeared in burnt areas, on a larger scale these burnt areas were still acting as grazing patches in the landscape. I suggest that this is due to the low rainfall; especially in December/January/February, when bunch grass is usually growing the fastest (Figure 4.10). Thus even though the grazing was dispersed over the entire areas of the burns, the grass was not growing rapidly enough to get above palatable height. The interactions between grazing, fire and rainfall are discussed further in Chapter 7.

Savanna systems are well known for being highly dynamic. They consist of a wide range of habitat and vegetation types; they are often in areas of very variable rainfall; and they are exposed to a range of disturbances, from large mammals, to fires, to humans. The processes creating and impacting on the spatial and temporal variability have been very difficult to unravel. This experiment gives some insight into these processes, especially the interactive/contingent effects of factors such as fire, grazing, and rainfall. It also indicates the importance of the spatial context in which these factors are operating. The results shown from this landscape-level experiment would have been very confusing without the spatial context of the effect of distance from a burn on grazer activity.

Heterogeneity, like biodiversity, has become a buzz-word; an ideal that managers and conservationists need to aspire towards when setting goals and implementing management policies. Like biodiversity it is hard to define, and even harder to preserve, because, by its very nature, it is variable in space and time. Two extensive bodies of literature exist, which discuss the importance of herbivory and the importance of fire in influencing heterogeneity. In this study I demonstrate an interaction between them. When grazing, a highly dynamic process, is affected by fire, itself very variable in space and time, the response of the vegetation results in patterns which are also dynamic. However these patterns are not chaotic: the mechanisms can be explained, and used to predict, to better effect, the consequences of alternative management policies and practices.

Chapters 5 and 6: preface

In chapters 3 and 4 I have shown how, on an annual time-scale, fires are affecting the distribution of grazing, and the persistence of grazed patches in the landscape. Next it is necessary to consider the long term consequences of this process. In the introduction (Chapter 1) I predicted that this mechanism could be affecting the degree to which lawn grasses spread in the landscape: i.e. that in the absence of fires, there would be areas in the landscape that are intensively, persistently utilised to a degree that bunch grasses diminish and lawn grasses spread; and that the seasonal changes in grazing patterns caused by fires will prevent this from happening in a system with many large fires.

To test this prediction it is necessary to have information on the spatial distribution of lawn-grasslands at HUP, to see whether this is related at all to the fire regime that the area has been exposed to in recent years. Chapter 5 describes the methods used to create the map from satellite imagery, and in Chapter 6 I investigate long term consequences of frequent large fires on the grass communities at Hluhluwe Umfolozi Park.

Chapter 5: Grass community classification from satellite imagery

Aim

To map the distribution of two grass community types (bunch-grass communities and lawn-grass communities) in Hluhluwe Umfolozi Park (HUP), Kwa-Zulu-Natal.

Introduction

Analytical approach

Most of the work on remote sensing of grasslands has involved picking up qualitative differences in species mixes (Goodin & Henebry 1997; Lauver 1997; Tieszen *et al.* 1997), looking at changes over time or over space (Nellis & Briggs 1989; Henebry 1993; Reed *et al.* 1994), or in assessing degradation and disturbance patterns (Ringrose *et al.* 1999); not in identifying clearly defined categories of grassland types (but see Asrar *et al.* 1986). This is because in natural grassland systems there is often no clear distinction between grass communities at most spatial scales. They are different from more human-controlled environments where land-use and land-cover types have clearly defined boundaries (Buttner & Csillag 1988). Hluhluwe Umfolozi Park is also a natural system with no clear boundaries, and the spatial distinction between the two grass communities is not always clear: lawn grasses are found within bunch-grass-dominated areas and vice versa. However, it is always possible on the ground to identify an area as functionally bunch grass or grazing lawn, so it is appropriate to attempt to classify the grass layer in this way.

Because of this, the techniques that I used were drawn more from the literature on mapping land-use e.g. (Buttner & Csillag 1988; Turner & Congalton 1998; Fairbanks *et al.* 2000). The aim was to identify each pixel as bunch-grass (BG), lawn-grass (LG) or Other – ignoring finer scale differences in proportions of grass species types within a pixel – so I did not attempt finer scale analysis or use mixture models.

In other ecosystems significant spectral differences between grass community types have been identified (Kremer & Running 1993). Thus at HUP I hoped that by identifying the key characteristics of the communities that would highlight spectral differences, and by choosing a time of year when the differences were most pronounced I would be able to achieve a satisfactory classification of the park.

The grass communities at HUP

The most obvious differences between the two grass communities are structural: Most lawn-grass species are short-statured, stoloniferous grass species, whereas bunch-grass species grow very tall (BG can be >1m tall, with 700g/m^{-2} standing biomass at end of the dry season, LG is generally not higher than 20cm, even when ungrazed, total standing biomass <200g/m2). These structural differences are further emphasised because heavy grazing occurs on the lawn-grass communities, so, especially by the end of the season, these lawns are grazed very short, whereas there is much less grazing in the bunch-grass areas, (generally these areas are only utilised during the dry season) and most of these areas are still tall at the end of the wet season. Another obvious difference is that lawn grasses have a very clear deterministic seasonal growth pattern: they remain green and actively growing until about April/May, and then stop growing until the next rains in September/October. Bunch grass communities on the other hand, generally have a lot of dry, dead material accumulated by the end of the wet season, because they grow faster than the material can be removed by herbivores (Downing 1974). Also, many bunch grass species (*Themeda triandra, Hyparrhenia filipendula, Cymbopogon excavatus*) are andropogonoid grasses, which have a reddish colour in their leaves even when they are still green.

At the end of the wet season (March/April) grazing lawn areas are grazed short. There is often some bare ground showing, but they are also still green with a high proportion of live material. Bunch-grass areas, on the other hand, have not been grazed short yet – there is a large amount of accumulated, dry, dead leaf-material, which is a reddish-brown colour (Plate G). Both grass communities are almost entirely C4 grasses so techniques developed to differentiate between C3 and C4 grass species are not pertinent here.

Plate G: *Showing differences between tall bunch grass and stoloniferous lawn grass communities.*

Thus I thought it was possible that these two community types would have significantly different spectral signatures on a Landsat TM satellite image to allow me to identify grazing lawn areas and bunch grass areas at Hluhluwe Umfolozi Park.

Landsat was chosen because, while its spatial resolution is quite coarse (30m), it has a high spectral resolution, with two infra-red bands, and this would be important when looking for differences between short, green, lawn grass areas and taller, dryer, reddish bunch grass areas: May *et al.* (1997) showed that Landsat TM images were more useful than finer-scaled SPOT images for classifying shrub and meadow vegetation, and Kremer & Running (1993) used coarse-scaled NOAA/AVHRR images successfully to classify sagebrush-steppe communities because they had infra-red spectral information. It was decided to compromise fine-scale resolution for the sake of increased spectral information, and therefore increased identification of the grassland types.

Use of single date classification rather than multi-temporal data was for simplicity and economy, but also because I did not believe that multi-temporal data would add much information. A study in semi-arid grasslands found single date classifications were always more accurate than simple multi-temporal ones (Langley *et al.* 2001), and the analysis by

Kremer & Running (1993) indicates that when grass communities senesce at different times (as at HUP) there are certain key periods during the year when the differences are greatest. This period occurs in April/May at HUP.

There are several examples where classification of grasslands has proved to be successful: (Asrar *et al.* 1986; Kremer & Running 1993; Goodin & Henebry 1997; Turner & Congalton 1998). However, there were some potential problems with a classification of grass community types at HUP:

- The tree layer: HUP is a savanna system with a prominent tree layer. It was likely that differences in tree species and tree densities might obscure similarities/ differences in the spectral characteristics of the grass layer underneath: I was hoping to achieve a classification that would identify areas as LG or BG even if they had very different tree layers, and to test this I used training areas with dense trees and with fewer trees and investigated how different the signatures were.
- Patch size: because the resolution of a Landsat image is only 30m, it would not be possible to identify areas of lawn grass that are smaller than that: Smith *et al.* (2002) show clearly how patch size affects Landsat TM classification accuracy. Thus, any map that I create is only identifying the larger grazing lawn area, not the smaller (2mx2m) patches of lawn grass that are often present in areas that are in the process of switching from one community state to another. However, as I show later, areas with frequent small lawn-grass patches could still be distinguishable from continuous bunch grassland – see results section.
- Short grazed bunch-grass areas: while I did say that most of the bunch grass is ungrazed at this time of year, you do get some areas of BG, especially in Umfolozi, which have been grazed short during the growing season. There is the possibility that these areas would be misclassified as LG. Thus this needed to be specifically investigated during the analysis.
- Landscape differences: topographic distortion, difference in rainfall (and therefore amount of water present) between the north (Hluhluwe) and the south (Umfolozi) might mean that the signatures of lawn-grass/bunch-grass are different in the two regions. Kremer & Running (1993) found that topography and slope affected the accuracy of their grassland classification. One way of getting around this problem would be to attempt a separate classification for Hluhluwe and Umfolozi to see whether this gives a better result.

Methods

I procured a Landsat TM satellite image taken on the 8 April 1999 from the Satellite Applications Centre of the CSIR. This image had no cloud cover and was already geo-referenced and rectified. I imported the image into Erdas IMAGINE software package and used a supervised classification procedure to create the map.

Jensen (1996) identifies 5 steps to the classification process:

- the identification of an appropriate land cover classification scheme,
- selection of training sites which characterise the spectral signatures of each category,
- identification of spectral bands/indexes to be used in the classification (feature selection),
- classification of the image using an appropriate classification algorithm,
- accuracy assessment.

1: Choosing a classification scheme

Before finalising a classification scheme I wanted to know whether the problems of variation in tree density, grass height, and geography were going to interfere with the classification. So I initially created nine grass community sub-categories to get information on which type of grasslands could be distinguished, and whether I was justified in grouping all bunch grasses and all lawn grasses together. Then I reduced the classification to broader categories when I found no difference between the sub-categories. I used the transformed divergence index to assess separability (ERDAS 1999). This value ranges from 0 to 2000. A value of above 1700 is a good separation, and above 1900 the classes are clearly separable (Jensen 1996).

Initial Categories:

Short (grazed) Andropogonoid Bunch Grass
Tall (ungrazed) Andropogonoid Bunch Grass
Andropogonoid Bunch Grass with dense trees

Short Chlorodoid Bunch Grass
Tall Chlorodoid Bunch grass
Chlorodoid Bunch grass with dense trees

Hluhluwe Lawn grass
Umfolozi Lawn grass
Seme Lawn grass (a large grazing lawn in the middle of the park).

2: Choosing training areas

I recorded the locations of the training areas using a hand-held AV Garmin GPS in the field. I used 23 training areas for grazing lawns and 38 training areas for bunch grasslands.

The aim was for the training areas to incorporate as much of the variation found within the two grass community types as possible: this variation was in the form of:

- Variation in the degree of tree cover
- Variation in the species of in the Bunch Grass communities: bunch grass areas are either dominated by *Themeda triandra* (Andropogonoid grasses) or *Sporobolus pyramidalis* (Chlorodoid grasses). It would be useful if these two grass types were also differentiable from satellite imagery.
- Variation in the species in the grazing lawns. This variation shows quite a clear geographic pattern: The species in the grazing lawns in Hluhluwe and in Umfolozi are generally quite different
    - Hluhluwe: *Digitaria longiflora, Dactyloctenium australe, Sporobolus nitens, Eragrostis superba, Chloris gayana.*
    - Umfolozi: *Urochloa mosambicensis, Panicum coloratum, Digitaria argyrograpta, Sporobolus nitens, Eragrostis superba, Sporobolus ioclados.*
- Variation in the amount of soil available moisture (Rainfall in the park ranges from 400-1200mm – this also has a geographic trend from north to south)
- Variation in altitude (altitude ranges from 0 to 560m above sea level in the park).

Except for a few of the lawn grass areas, which had a bimodal distribution in band 4, the spectral data was normally distributed (visual inspection of histograms) for all bands and for all training areas (Mather 1999)

3: Feature selection

A visual inspection of histograms indicated that bands 4, 3,and 2 gave the best separability between classes. I used all landsat bands (except band 6-thermal band) to assess the separability of the spectral signatures. I did not use any vegetation indices; although it is possible that using NDVI, or tassled cap transformations would have been useful, the accuracy of the results do not make this essential (see accuracy assessment).

Results of separability analysis

An initial separability analysis using all 9 subcategories clearly separates all lawn grass categories from all bunch grass categories (one exception: short CBG not significantly differentiable from HLG - Table 5.1). There is no significant difference between the signatures of lawn grasses from the three different areas so I am justified in grouping them together.

***Table 5.1:** Summary of results of initial separability analysis on different grassland categories*

		Andr. BG-wtrees 1	Andr. BG-tall 2	Andr. BG-short 3	Chl. BG-short 4	Chl. BG-tall 5	Chl. BG-wtrees 6	Hlu. LG 7	Umf. LG 8	Seme LG 9
Andr. BG-wtrees	1	~	*	*	*	*	*	*	*	*
Andr. BG-tall	2		~	ns	ns	ns	*	*	*	*
Andr. BG-short	3			~	ns	ns	*	*	*	*
Chl. BG-short	4				~	ns	*	ns	*	*
Chl. BG-tall	5					~	*	*	*	*
Chl. BG-wtrees	6						~	*	*	*
Hlu. LG	7							~	ns	ns
Umf. LG	8								~	ns
Seme LG	9									~

There is no significant difference between short and tall bunch grass categories, which is important because it means that bunch grass areas that have been grazed short can still be identified as bunch grass (i.e. the classification is going to be picking up grass community types, not just ephemeral differences).

The differences between Chlorodoid and Andropogonoid grass signatures are not significant. However, bunch grass areas with dense trees have a very different signature from areas with a lower tree cover. This is to be expected as trees would have a big impact on the spectral signature (Hudak & Wessman 1998).

Even though this initial analysis indicates that Chlorodoids and Andropogonoids aren't different, and areas with dense trees are different, that is not what I was trying to classify. So my next step was to test the separability of the three different categories that I was hoping to identify in the landscape: I grouped all subcategories together and created an Andropogonoid Bunch Grass signature, a Chlorodoid Bunch Grass signature and a Lawn Grass signature.

The separability index of these three categories is listed in Table 5.2: a contingency matrix indicates the degree of overlap between the signatures (Table 5.3).

***Table 5.2:** Best average separability between the spectral signatures for three grass community types at HUP*

Comparison	*Separability*
LG: Chlorodoid BG	**1673**
LG: Andropogonoid BG	**1817**
Chlorodoid BG:Andropogonoid BG	839

***Table 5.3:** Contingency table showing the number of pixels which overlap in their spectral signatures*

Classified Data	*Reference Data* **LG**	**Chlorodoid BG**	**Andropogonoid BG**	**Row Total**
LG	538 (79%)	24	161	723
Chlorodoid BG	143	199 (64%)	330	672
Andropogonoid BG	3	88	892 (65%)	983
Column Total	**684**	**311**	**1383**	2378

Lawn grasses are clearly different from both Bunch Grass categories (but more different from andropogonoid BG than from chlorodoid BG– which is understandable as andropogonoids have the distinctive reddish pigment, and as tussocks of chlorodoid bunch grasses are sometimes found in grazing lawns. The two bunch grass communities are not different from each other (>25% overlap - Table 5.3).

Finally, because there is no difference between the two bunch grass sub-types, I tested the separability of all BG from all LG:

Transformed Divergence of the LG signature from the BG signature was 1778 which indicated adequate separability (Jensen 1996). A contingency matrix indicates the degree of overlap between the two signatures (Table 5.4): less than 10% of the pixels overlap.

***Table 5.4:** Contingency table showing the number of pixels which overlap in their spectral signatures*

Classified data	*Reference Data* LG totcomb	BG totcomb	Row Total
LG totcomb	622 (91%)	121	743
BG totcomb	62	1573 (93%)	1635
Column Total	684	1694	2378

Thus lawn grass areas are statistically differentiable from bunch grass areas based on their spectral information, and I am justified in performing a classification of the park into LG, BG, and OTHER.

Also, even though the two bunch grass communities are not statistically differentiable I also performed a classification between LG, Andr. BG, Chl. BG, and OTHER, to see whether the resulting map would represent the known distributions of andropogonoid and chlorodoid communities.

4: Classification methods

The procedure was as follows:

- First I classified all pixels according to a non-parametric **parallelepid limits decision rule** (setting the limits to maximum and minimum values).
- Pixels which were unclassified by this rule remained unclassified (i.e. they did not fit the spectral characteristics of either grass community. These were classed 'other' in the final map).
- Pixels whose signatures overlapped two categories were classified according to the **Maximum Likelihood decision rule**: This rule is the most accurate (providing that assumptions of normality are met) and as I expected that many pixels would overlap, it was the most appropriate. As mentioned earlier, the training sample data was normally distributed. However, it is necessary to assign prior probabilities because there is much less lawn grass in the park. Mather (1999) suggests that to estimate these probabilities one can use an unsupervised classification, and my unsupervised classification identified about 7% of the park as LG. I used prior probabilities of 0.1 for lawn grass.

5: Accuracy assessment: methods

The map used for the accuracy assessment was the statistically-significant simpler map which identifies LG, BG, and OTHER. The accuracy of the map which differentiates between Andropogonoid BG and Chlorodoid BG areas has not been tested.

Identifying grazing lawn test points

I did not want to test the accuracy of individually identified pixels, nor is this possible to do accurately (Congalton 2001). I was interested in whether the map could identify grazing lawn areas, so I chose polygons to be my sampling unit (Congalton 2001). I converted the map to a polygon shape file, calculated the area of each lawn-grass polygon and isolated all polygons greater than or equal to 5 Ha and within 800m of a road (this last was to make sampling more efficient –Fairbanks & Thompson 1996).

The lawn grass areas are not evenly scattered through the park, but I wanted to test the accuracy of the classification in all areas of the park, to ensure an evenly spread sample. So, as a form of stratified random sampling (de Gruijter 1999; Congalton 2001) I separated the park into three areas: Hluhluwe, Umfolozi, and Wilderness, and using the script: *view.randomselection* I randomly identified 25 test sites in each area. If a site was precisely on a road, or within 500m of another test site I did not use it. I chose 25 sites in each area (i.e. 75 sites in total) because it was likely that some sites would be excluded or inaccessible, and the aim was to have at least 50 test points per grass community type (Fairbanks & Thompson 1996; Jensen 1996; Congalton 2001).

At each test site I marked three test points to be located and described. This was in order to encompass some of the heterogeneity of the grazing lawn areas, and to allow for a degree of inaccuracy (approximately 10m) in locating the sampling site by GPS (Fairbanks & Thompson 1996).

Identifying Bunch Grass test points

The procedure for bunch grass areas was slightly simpler because most bunch grass areas are large and homogenous. I isolated all bunch grass pixels within 800m of a road, then, for each of the three geographic areas I randomly selected 25 BG pixels by using a random grid. If the test pixel was surrounded by other BG pixels, and not within 500m of another BG test pixel it was included.

So I ended up with a selection of 150 test sites, half lawn grass half bunch grass spread as evenly as the road system will allow throughout the park (Figure 5.1).

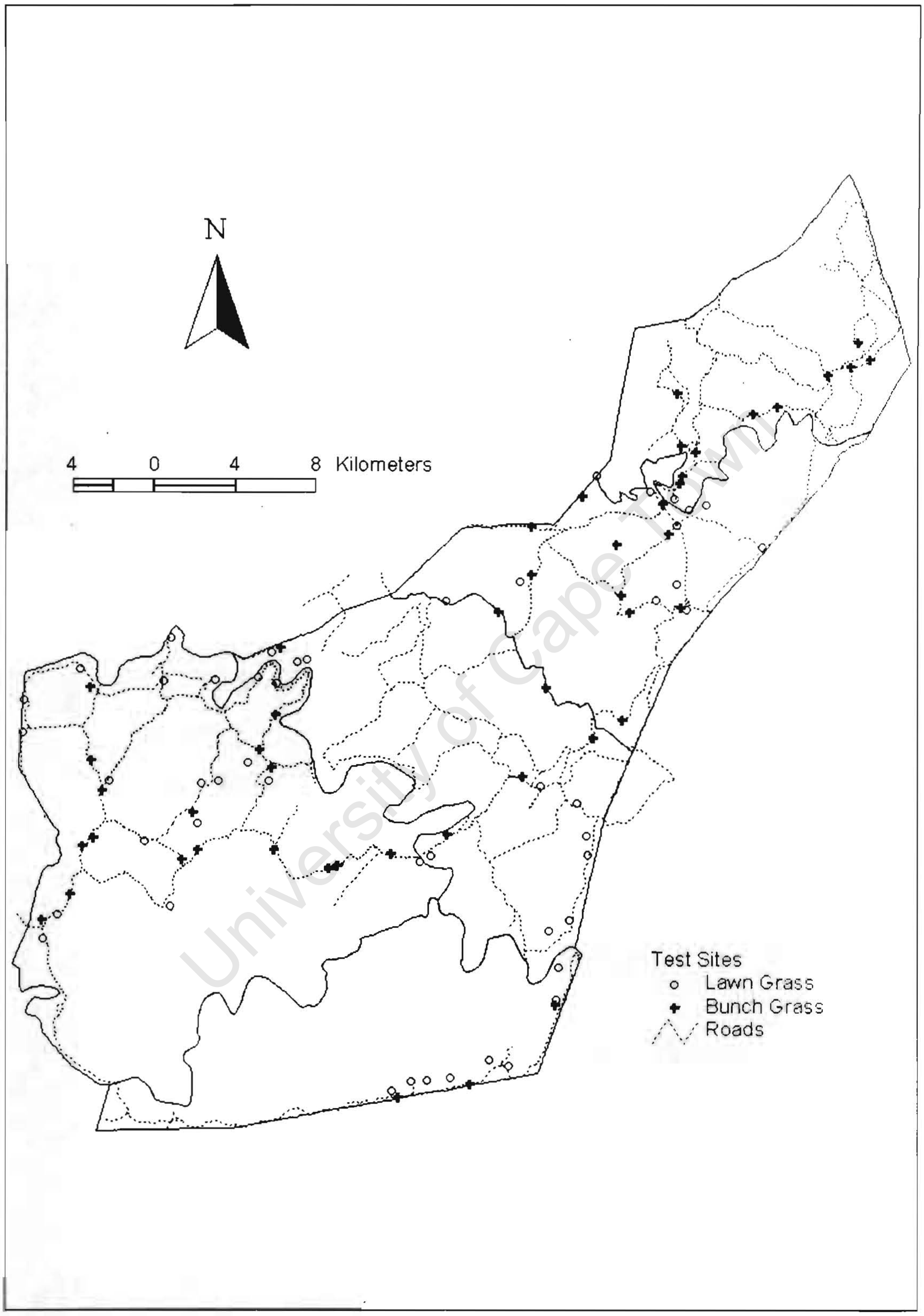

Figure 5.1: *A map of HUP showing the road system and the location of the test sites which were used in the accuracy assessment of the vegetation classification.*

Groundtruthing

I then groundtruthed the data. Using a Garmin GPS (accuracy 10m) I walked to each test point. At each test point I recorded:

- Grass community type (Bunch grassland, Grazing lawn, 'other'),
- Grass height in 2002, (tall/short, tall grass is >10cm. This could have been very different in 1999)
- More detailed information about the type of grassland i.e.
    - For bunch grass:
        - Andropogonoid-dominated
        - Chlorodoid-dominated
        - Panicoid-dominated
    - For Lawn grass:
        - grazing lawn
        - grazing lawn with a few BG patches/tussocks
        - frequent patches of LG (bigger than 20x20m) within BG
        - LG present but not enough to be classified as a LG community
        - no LG at all
    - For 'Other'
        - Rocky/eroded bare ground
        - Dongas
        - *Chromolaena odorata* infested area
- Tree density category (open grassland, encroached grassland, open woodland, closed woodland, forest).
- Degree of grazing (measured from 0 - no bites, to 4 - all grass bitten)
- The main grass species present.

With this information I would be able to produce an error matrix of broad grass community groupings, but also find out how precise the identification of grazing lawn areas was: i.e. did the satellite image only pick up grazing lawns, or could it identify areas that had large lawn grass patches within a bunch grassland? It would also help to identify particular types of LG or BG which were prone to being misclassified

I ended up sampling 49 of the lawn-grass test sites, and 47 of the bunch-grass test sites.

Results

The two maps produced are shown in Figures 5.2 A and B.

Most of the park is classified as bunch grassland. This is because the signatures for bunch grassland with dense trees were included in the classification: a lot of the park consists of a savanna woodland with a bunch grass under-story (Brooks & Macdonald 1983).

The overall accuracy of the map is 85.4 percent, which is acceptable. Most classifications aim for an accuracy of >85% (Fairbanks & Thompson 1996). The Khat(Kappa) coefficient is also good: 81.1% - values of >80% represent strong agreement of classification with reference data (Congalton 2001). This is important as the proportions' of the different grass communities in the park are very different, so the Khat is a better indication of the accuracy of the classification (Mather, 1999; Langley *et al.* 2001). The producers' accuracy is very good for LG (97.4%) i.e. if an area is a LG area it is likely to be classified as LG; but the users' accuracy is less good: if a site is classified as LG it was only found actually to be LG 78% of the time. However, this is a higher accuracy than has been reported in other attempts to classify grasslands (Turner & Congalton 1998; Langley *et al.* 2001).

Other land-covers that were misclassified as LG were dongas and rocky open areas (4 of the 49 sites selected were dongas). This is not really problematic as there are relatively few of these land-covers in the park, so they are not likely to interfere with any analysis we might want to use the map for. However, some bunch grass areas were also misclassified as lawn grass (7/49). The reasons for this misclassification of LG as BG could be two-fold: it could be that the BG was grazed so short that it gave a signature of LG, but it could also be that at the time the map was made, almost three years ago, there was more lawn grass at that site. This is quite likely because in 5 of the 7 misclassified sites there was lawn grass recorded as present - just not in significant enough quantities to be classified as a lawn grass site (also 5 of the 7 misclassified sites were tall, ungrazed grassland, not short bunch-grassland). This is an indication of what a dynamic system we are dealing with. It would be very interesting to use a time series of satellite images to describe the changes in the proportions of these grass communities over time.

Table 5.5: *Error matrix for the classification of grass community types at HUP*

	predicted grass community			
actual grass community	LG	BG	other	sum
LG	38	1	0	39
BG	7	44	0	51
Other	4	2	0	6
Sum	49	47	0	96
overall accuracy	**85.4%**			
Khat coeff	**81.1%**			

class	**producers accuracy**			**users accuracy**		
		%	% ommission error		%	% commission error
LG	38\39	97.4	2.6	38\49	77.6	22.4
BG	44\51	86.3	13.7	44\47	93.6	6.4

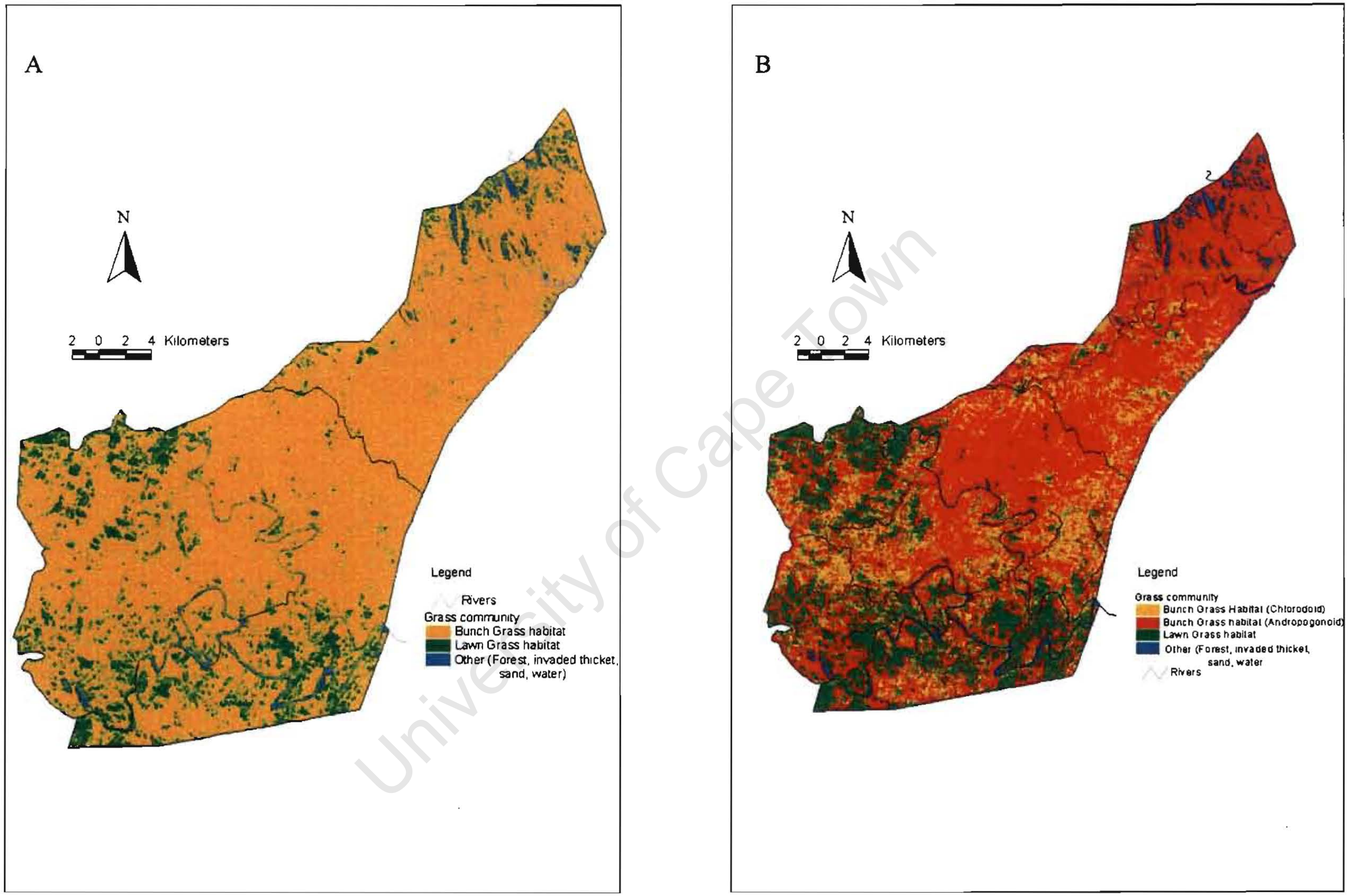

***Figure 5.2**: Maps of the distribution of bunch grass communities and lawn grass communities at Hluhluwe Umfolozi Park. Map A distinguishes between bunch grass and lawn grass, map B distinguishes further between the two main bunch grass types: those dominated by andropogonoid grasses and those dominated by chlorodoid grasses. Classified from LANDSAT TM satellite imagery using a supervised classification in ERDAS. Accuracy of map A is 85.4%, Khat co-efficient 81.1%, accuracy of map B has not been tested.*

Discussion

Potential problems: were they realised?

The final map has a very high accuracy and can confidently be used in spatial analysis of the park. However, which of the possible problems have proved to be important, and are there ways of solving them?

Tree layer

A comparison of the spectral reflectances of areas with similar grass layers but different densities of trees showed that, as expected, the tree layer did result in a significantly different spectral signature. However, this is not necessarily a problem, as long as areas of different grass communities but similar tree densities are also spectrally distinct. This seems to be the case, although generally the tree layer does not get as dense in lawn grass areas. Therefore the final map which was produced is only distinguishing between grass communities, not giving any information about the broad structural differences in vegetation (there are plans to create a structural map of the park from satellite imagery, in which case the grass-community map and the structural map could be combined). Thus only the areas of the park that have no grass at all: forests, densely encroached chromolaena thicket, sand and water, are excluded from the classification.

Patch size

Smith *et al.* (2002) showed convincingly that patch size and landscape heterogeneity can affect the accuracy of a satellite-derived map: classification accuracy decreases as patch size (number of contiguous pixels of the same land-cover type) decreases. Because each pixel is 30m x 30m, I did not expect to be able to identify a grazing lawn unless it was at least 90m x 90m (0.81 Ha). Thus small patches of lawn grass embedded within other grassland habitats are not going to be represented on the map. This was not a problem for the large grazing lawn areas like Seme, but many grazing lawn areas in Hluhluwe Umfolozi Park consist of a number of patches of lawn grass smaller than 90 x 90m that are scattered within a matrix of bunch grass. However, the accuracy assessment showed that areas which are dominated by large, (at least 20x20m) lawn-grass patches are still picked up by the classification, presumably because the spectral signature of these areas is different enough from homogenous bunch-grassland to be distinguishable. Thus the map can identify areas that are functioning lawn-grass communities. It does not give information on areas that are potentially becoming grazing lawns (very small very scattered lawn grass patches), or where bunch grasses have encroached grazing lawns.

Short-grazed bunch grass areas

The signature analysis showed that short bunch grass had a different signature from short lawn grass (Table 5.1). A few of the short bunch-grass sites were classified as lawn grass, but not all of them. I don't think I have established conclusively that the map distinguishes clearly between these two types.

Landscape/geographic differences

The analysis shows that none of the potential problems related to rainfall differences and geographic differences were realised. Spectral signatures between the same grass communities in different parts of the park were never significantly different from each other.

Conclusion

It is possible that a more detailed classification - using other vegetation indices and band ratios - would be able to be even more precise, and would decrease the number of mis-classified pixels even further (Tables 5.4 and 5.5). However, as mentioned in the introduction, in any natural system there are no clear boundaries between vegetation types, particularly between grass communities, and the aim of any classification is to serve a particular function, rather than to represent reality. I believe that my map will be reliable for the purpose for which it was made, which was to determine the spatial distribution of lawn grassland on a landscape scale.

Chapter 6: Are large, frequent fires limiting the spread of grazing lawns at HUP?

A landscape-level analysis of the long term effects of fire in a savanna system.

Introduction

The hypothesis that I am trying to test, as laid out in the introduction (Chapter 1), predicts that large frequent fires would limit the extent of grazing lawns in mesic grasslands. In previous chapters I have discussed the mechanism involved, and shown that fire is preventing grazed patches from persisting in the landscape. In this chapter I will investigate whether there is any indication that this process has indeed had an effect on grass community proportions and distributions in Hluhluwe Umfolozi Park: specifically whether the spatial distribution of lawn grasslands in the park is restricted by the fact that large areas of the park have been frequently, intensively burnt in the last 50 years.

The distribution of grazing lawns in an area is likely to be affected by numerous factors: anything which can have an impact on grass growth or on grazing patterns. However, I was interested in knowing whether, in the face of these other variables, the fire regime of the park was also a significant factor. It is an important question because, contrary to many other environmental factors, fire is something that it is possible and necessary to manage. I am suggesting that over time, grass communities, and therefore also habitat-distributions, can be affected strongly by the fire regime of an area. If so it is something that should be considered when one is setting up burning protocols.

This was a question that needed to be asked on a landscape scale, so I needed spatial data both on grass community distributions and on the burn history of the park. I have discussed in Chapter 5 how I created a map of the distribution of lawn and bunch grasses in the park. Balfour & Howison (2003) have created a map which shows, at a 50m resolution, the number of fires during the period 1956 to 1996. From this map I was able to isolate information on the burn history of any point in the park for the last 41 years.

I wanted to find out three things:

Firstly, is the extent of grazing lawn communities in an area related to the fire history of the area? In other words, do areas which have had very frequent fires in the last 40 years have a smaller proportion of lawn grass communities than would be expected if fire regime was not affecting the spread of grazing lawns?

Secondly, how important is fire regime as a predictor of lawn grass distribution in relation to other environmental factors which are known to be important? Slope, aspect, elevation, distance to water have all been identified as important factors affecting the distribution of grazing at a landscape scale (Senft *et al.* 1987; Pearson *et al.* 1995; Brock & Owensby 2000), while soils and rainfall are also likely to determine grass community composition - (O'Connor 1994; O'Connor & Bredenkamp 1997; Fynn & O.Connor 2000). In fact, in the Kruger National Park and other savanna systems it is suggested that soils are the main determinant of plant communities (Webber 1979; Bell 1982; Scholes & Walker 1993). If this is true, then the distribution of lawn vs. bunch grasslands would be correlated more with soil type than grazing intensity.

Thirdly, I compared two adjacent areas which had been burnt more, and less frequently in the last 40 years, and investigated whether there is any indication that lawn grasses are spreading into grazed patches in infrequently-burnt areas more than they are in frequently-burnt areas.

Methods

Relative proportions of lawn grass

Figure 5.2 in Chapter 5 shows the distribution of lawn and bunch grasslands at HUP in 1999. Figure 6.1 (this chapter) shows the number of fires in the last 41 years (Balfour & Howison 2003). Fire frequencies range from 1 to 25 fires between 1956 and 1996; i.e. the fire return interval ranged from 1.6 years to 41 years.

I looked at the relative proportions of lawn grass and bunch grass in areas which have experienced different fire return intervals. I combined all the areas in the park which had had the same number of fires and, by superimposing the vegetation map on the fire history map, calculated the total area of lawn grass and bunch grass for each fire frequency. I then calculated the proportion of lawn grass present for each fire frequency: i.e. I calculated: *area lawn grass / (area lawn grass + area bunch grass).*

I excluded areas with only one or two fires from the regression analysis because these were either located in dense forest (proportions of LG/BG immaterial) or else were on the edges of the map and were a result of digitising errors. They also did not represent a large proportion of the park (414 Ha all together, which is 0.46% of the park – Figure 6.4B). Those areas which had had more than 19 fires in the last 41 years were also not widespread (383 Ha, 0.43% of park-Figure 6.4B) but they were included in the analysis because they were located in areas of fire-prone grassland, and therefore represented one extreme of the gradient that I was trying to encompass.

Regression analysis

To investigate the effect of fire history in the context of other environmental factors I needed spatial data for all potential predictor variables. From a contour map of the park I created a 50m resolution Digital Elevation Model (DEM) using ARCINFO. From this I derived 5 more maps (all at 50m resolution) of slope, aspect, Topographic Wetness Index (TWI), Topographic Relative Moisture Index (TRMI) and Relative Slope Position (RSP). The two wetness indices are derived from models of how water accumulates in a topographic landscape (Parker 1982; Moore *et al.* 1991) and predict which areas are likely to have more soil water than others. The relative moisture index makes these values relative to the rest of the topography and is a slightly more sophisticated measure. Relative Slope Position was derived from the slope map, simplifying the map into ridges, hill-slopes and valleys.

Using the 'calculate distance' function in ARCVIEW I created a 50m resolution map of the distance to permanent water. I also scanned a 1: 250 000 geology map of the park, rectified the image, and digitised it on screen (Figure 6.2). The original map had 12 different geology categories, many of them a mixture of sandstone/shale. Dolerite produces clay-rich fertile soils in this region. The shale also produces fine-textured, often duplex soils, interspersed with areas of grey hydromorphic, relatively infertile sands and sandstone outcrops. To make the geology map tractable for predicting grazing lawns I simplified the map into three categories: "dolerite", "sandstones & shales", and "other" (granite, breccia, tillite, amygdaloidal basalt lavas, alluvium).

I ran a logistic regression to try to explain the distribution of lawn-grassland and bunch-grassland in the park (binomial dependent variable). My predictor variables were: altitude, slope, aspect, TRMI, TWI, RSP, geology, distance to permanent water (square-root transformed) and fire history. Altitude not only potentially affects grazing patterns in its own right, but it has been shown to be correlated with rainfall both in the park (r^2 0.94, $p< 0.001$ – Balfour & Howison 2003) and on a regional scale (Dent *et al.* 1989). Thus I use altitude as an indicator of rainfall, which, because it affects growth rates, is likely to be important in determining whether bunch or lawn grasses dominate in an area (Swemmer 1998).

As can be seen in Figure 5.2, bunch grass covers a much greater area of the park than lawn grass, and the lawn grass is concentrated in the south of the park. Therefore I did not stratify my sampling, but ensured that the proportions of LG:BG sample points were the same as the proportion of LG:BG in the park (10%). Using a grid of random numbers I randomly selected c. 5 000 sample points in ARCVIEW, and out of these again randomly selected c. 2000 points for creating the regression model. The rest of the points were used in cross-validation of the model. Therefore my analysis sample consisted of 169 LG points and 1655 BG points.

Some of the predictor variables were correlated (Table 6.1), so I removed TWI, and RSP from the analysis. However, I did not remove altitude from the analysis.

***Table 6.1:** Correlations between different predictor variables*

	(DIST_RIVER)^0.5	FIRE_HIST	ALTITUDE	SLOPE	ASPECT	TRMI	TWI	RSP
(DIST_RIVER)^0.5	1	0.33	0.41	0.20	0.18	-0.14	-0.30	-0.01
FIRE_HISTORY	0.33	1	**0.54**	0.34	0.13	-0.12	-0.26	-0.08
ALTITUDE	0.41	**0.54**	1	**0.54**	0.25	-0.25	-0.53	-0.23
SLOPE	0.20	0.34	**0.54**	1	0.27	-0.25	**-0.59**	-0.01
ASPECT	0.18	0.13	0.25	0.27	1	-0.18	-0.39	-0.10
TRMI	-0.14	-0.12	-0.25	-0.25	-0.18	1	0.45	**0.60**
TWI	-0.30	-0.26	-0.53	**-0.59**	-0.39	0.45	1	0.49
RSP	-0.01	-0.08	-0.23	-0.01	-0.10	**0.60**	0.49	1

Non-parametric approach

I also used the same data and all of the independent variables in a non-parametric classification tree procedure which uses hierarchical decision-making criteria to predict the occurrence of lawn/bunch grass. For this analysis I used equal numbers of LG and BG points (STATISTICA electronic manual). I used the C&RT style exhaustive search for univariate splits, and fact-style direct stopping procedure (fraction of observations 0.25), and also tested the results with a different set of validation data.

Road-transect comparison

One section of the park provided the opportunity to do a more detailed comparison of the differences between frequently- and infrequently-burnt areas. In the Mbuzane section in the south of the park a road divided two areas which were similar in all respects except that one side had been burnt 14 times in the last 41 years, while the other side had been burnt less than 5 times (the road had acted as an accidental fire break) - Figure 6.3. Thus it was possible to compare the distributions of the grass communities, and the characteristics of the grass sward, on either side of the road with the assumption that any differences encountered would be due to the difference in fire return interval (ca. 3 and 8 years respectively).

Neither side of the road had been burnt during the previous fire season. In June 2001 I walked two transects on each side of the road and recorded the following: the proportion of lawn grass in every 50m sample; the amount of grazing (0= no grazing, 1 =a few bites, 2=more unbitten than bitten, 3=more bitten than unbitten, 4=a few unbitten, 5=no unbitten); an index of tree cover (0=open grassland, 1=encroached grassland, 2=open canopy woodland 3=thicket, 4=closed canopy woodland).

Results

Relative proportions of lawn grass

Figure 6.4A shows the proportion of lawn grass in relation to the number of times the area was burnt between 1956 and 1996. Areas which have burnt infrequently have more lawn grass than would be expected from the proportions in the whole park. Areas which have burnt often have very little lawn grass. A regression fitted to this relationship has an r^2 of 0.94.

Logistic Regression analysis

The best fit model, tested using forwards stepwise, backwards stepwise, and best subsets model-building procedures, was one which included the following 4 factors:

1. FIRE HISTORY,
2. SLOPE,
3. TRMI (Topographic Relative Moisture Index),
4. DISTANCE TO RIVER (square-root transformed)

(in order of significance, see Table 6.2).

***Table 6.2**: Results of the best fit model for grass communities at Hluhluwe Umfolozi Park. Four factors are significant predictors of lawn grass distribution. Estimates, and upper and lower confidence limits for the co-efficients are given.*

	Wald Stat.	p	Estimate	St. Err.	lower 95% CL	Upper 95% CL
Intercept	0.86	0.3541	0.454	0.490	-0.506	1.414
FIRE_HISTORY	**38.77**	**0.0000**	**-0.188**	**0.030**	-0.247	-0.129
SLOPE	**15.07**	**0.0001**	**-0.108**	**0.028**	-0.163	-0.054
TRMI	**9.43**	**0.0021**	**-0.034**	**0.011**	-0.055	-0.012
(DIST_RIVER)^0.5	**6.10**	**0.0135**	**0.017**	**0.007**	0.004	0.031
Scale			1	0		

Fire history was found to be one of the most important predictors of lawn grass distribution. Table 6.3 shows the two best models for each degree of freedom from the best subset model-building procedure. Out of the 1-factor models, fire history was the single best predictor variable, and the best 2,3,and 4-factor models all included fire history. In fact, out of 112 potential significant models, the best 48 models all included fire history.

Table 6.3: Comparing different possible models created by the best-subset model building procedure. The Akaike Information Criterion is an index used to compare possible models. It is based on log-likelihood score, but includes a measure of degrees of freedom – (Akaike 1983). Fire history is the best single variable, and is also included in all other best subsets.

model predictive power (ranked value from 1 to 112)	factors				df	AIC (Akaike Information Criterion)	L. Ratio Chi2	p
1	**(DIST_RIVER)^0.5**	**FIRE_HISTORY**	**SLOPE**	**TRMI**	**4**	**1033**	**89.5**	**0.000**
13	(DIST_RIVER)^0.5	FIRE_HISTORY	ALTITUDE	SLOPE	4	1040	82.1	0.000
9	**FIRE_HISTORY**	**SLOPE**	**TRMI**		**3**	**1039**	**81.6**	**0.000**
29	(DIST_RIVER)^0.5	FIRE_HISTORY	ALTITUDE		3	1046	74.5	0.000
31	**FIRE_HISTORY**	**SLOPE**			**2**	**1047**	**71.5**	**0.000**
42	(DIST_RIVER)^0.5	FIRE_HISTORY			2	1049	68.8	0.000
57	**FIRE_HISTORY**				**1**	**1054**	**61.9**	**0.000**
101	SLOPE				1	1084	32.0	0.000

The 4-factor model was 64% accurate in its identification of lawn and bunch grass points, and had a 65% accuracy when tested using the cross-validation sample. I used this model to predict grass community distributions in the park under different fire regimes. In ARCVIEW, I back-predicted the potential distributions of lawn and bunch grasslands if the entire park had been exposed to a uniform fire frequency of 6, 9 and 13 fires in the last 41 years (lower 75%, median, and upper 75% respectively- Fig 6.4B). Figure 6.5 shows the results of this prediction.

Figure 6.6 shows the best classification tree produced by the non-parametric procedure. The classification was 71% accurate, (84/334 cases misclassified), and the test sample was 60% accurate (578/1423 cases misclassified). It is similar to the parametric logistic-regression result in that fire history, slope, distance to river, and TWI (equivalent to TRMI) were important predictors. Figure 6.7 ranks the importance of the different variables as determined by the classification.

Road-Transect comparison

In total, 29.4% of the transect on the frequently burnt side of the road consisted of lawn grass areas and 35.4% of the infrequently burnt side consisted of lawn grass areas. The difference between these values was not significant. However, the size and spatial distribution of lawn grass patches on either side of the road was very different. The grazing lawn areas on the frequently burnt side of the road were generally large, permanent parts of the landscape, and had obviously been there for a very long time, and they were interspersed in areas of continuous bunch-grassland. The grass sward on the infrequently burnt side was much more patchy: many small patches of lawn grass were found scattered within the bunch-grassland, and there were also some larger, older grazing lawns.

Figure 6.8 shows this difference graphically. Data was collected in 50m sample intervals and the proportion of grazing lawn patches in each 50m was recorded. Areas which contain large grazing lawn areas (>=50m diameter) would have a large proportion of sample intervals with 80-100% lawn grass, and areas with smaller (<50m) patches of lawn grass would have more sample intervals containing 20-80% lawn grass. In pure bunch grass areas, with no lawn grass patches, most of the sample intervals would have 0% lawn grass. Therefore, the frequency distributions of the %lawn grass in a sample interval shows how the spatial characteristics of the grazing lawns differed in each transect.

I tested for differences between these frequency distributions using a Mann-Whitney U test (z=2.33, p=0.019).

The amount of grazing on either side of the road was also found to be different (Figure 6.9). More of the infrequently burnt side had been exposed to heavy grazing in the last year than had the frequently burnt side.

Geology

Table 6.4 lists the different geological formations at HUP and shows the total area of each geological type in the park, together with the total area of lawn grass in each geological type. These values were calculated in ARCVIEW using the geology map and the grass community map. Lawn grasses do not seem to be limited to any particular geology type, and no geological area has very much more or less lawn grass than would be expected based on its area in the park. It is especially noticeable that the granite, breccia and basalt areas have less. rather than more lawn grass than the calculated expected proportion. Work in other parks in SA would lead us to expect that lawn grasses would be predominantly found on these geology types, and on the dolerite extrusions. This data therefore suggests that at Hluhluwe Umfolozi Park lawn-grass distribution is not strongly influenced by soils, and this is corroborated by the regression analysis which does not isolate geology as a significant predictor.

Table 6.4: *Geological types at Hluhluwe Umfolozi park and the distribution of lawn grass areas. Calculated from the geology and the grass community maps using ARCVIEW.*

GEOLOGY	total area (Ha)	area lg (Ha)	expected area lg (Ha)
alluvium	187	3	7
amydaloidal basalt lavas	717	0	27
breccia dykes	101	1	4
conglomerate sandstone shale	1991	34	74
dolerite and dolerite dykes	14268	673	531
granite	987	0	37
mudstones shales and sandstones	1072	27	40
sand stones, shale	53214	2223	1981
sandstone, shale, coal	4091	18	152
sandstones, some shales	812	19	30
shales, thin sandstones	9015	207	336
tillite breccia	3045	128	113
Total	**89500**	**3332**	**3332**

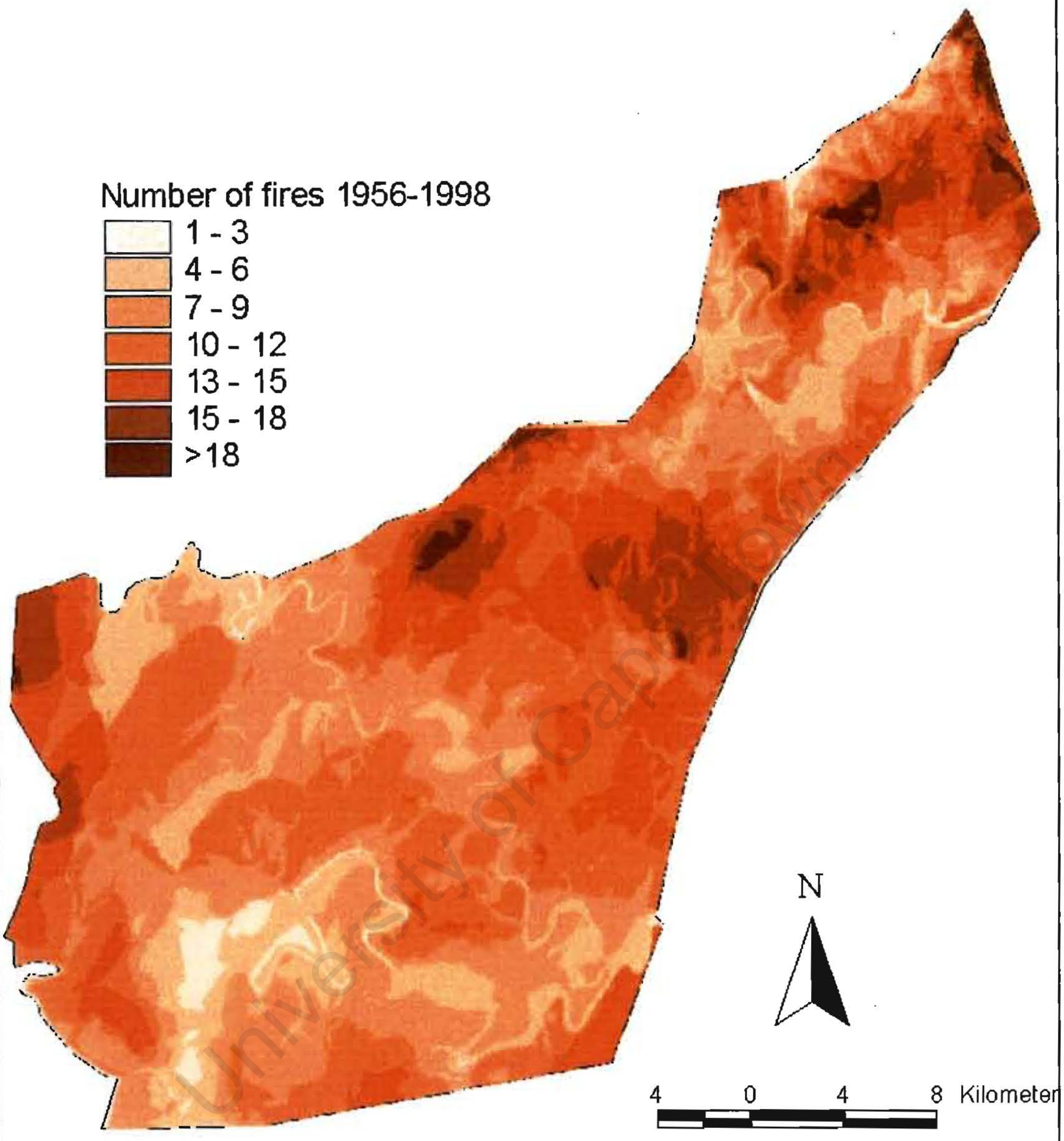

***Figure 6.1**: Map showing the spatial variation in fire frequency in Hluhluwe Umfolozi Park: the number of fires between 1956 and 1998 (Data from Balfour & Howison 2003).*

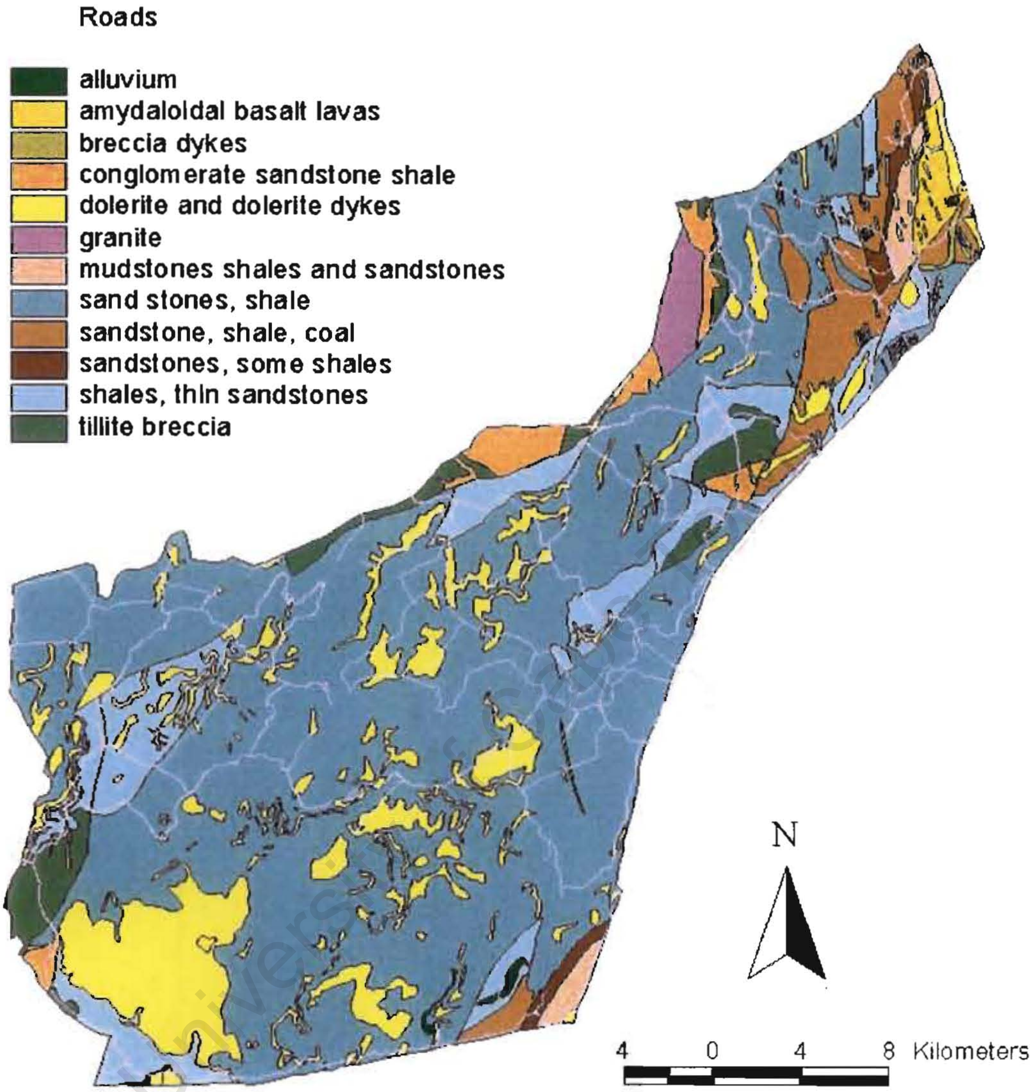

***Figure 6.2**: Geology of Hluhluwe Umfolozi Park (digitised from 1:250 000 geology maps)*

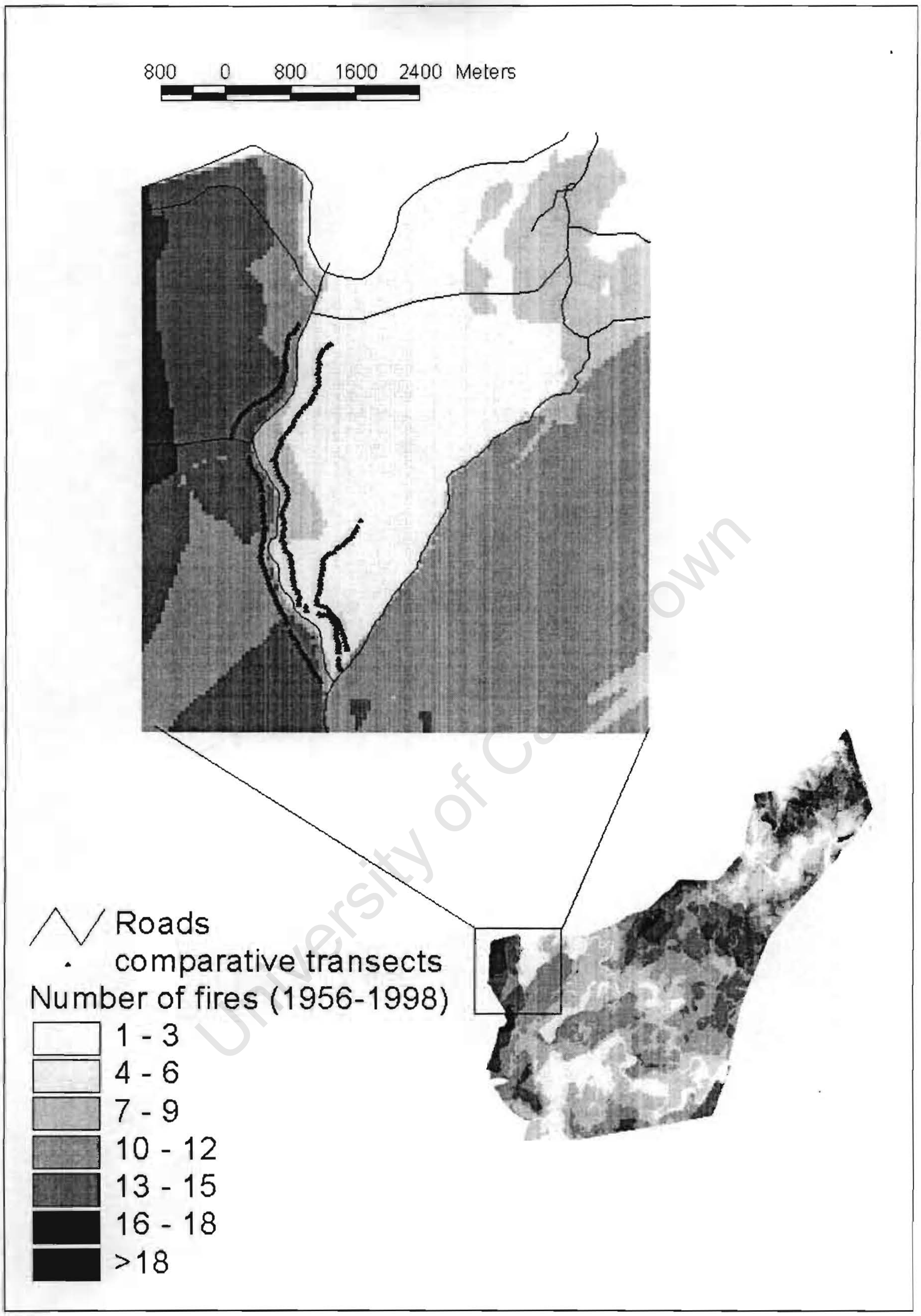

__Figure 6.3__: Location of a road-side comparison between frequently and infrequently burnt grasslands at HUP

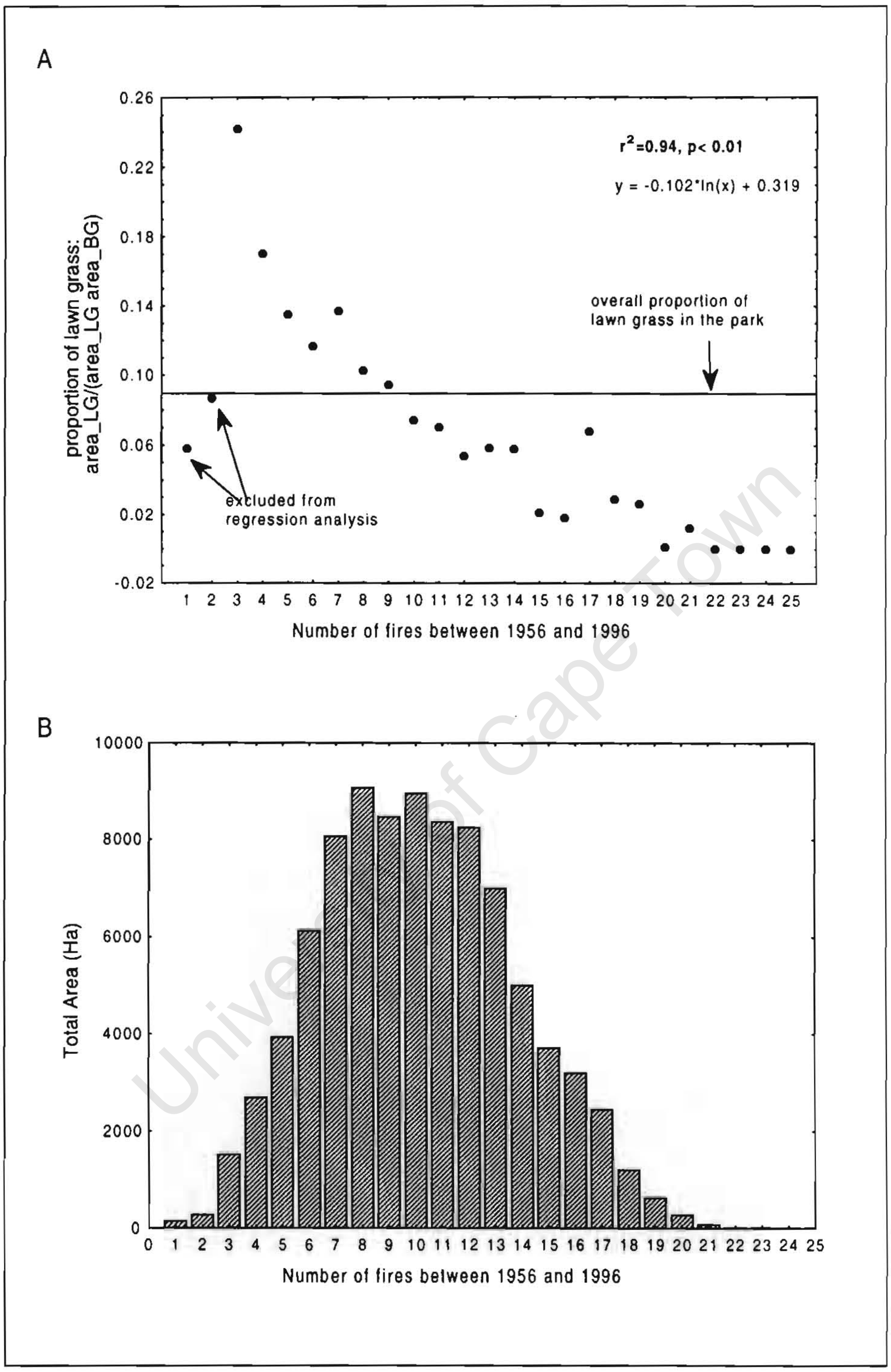

Figure 6.4: *A - The proportion of lawn grass represented in areas which have had different fire return intervals in recent years. Areas which have burnt very seldom have more lawn grass than would be expected, and areas which have burnt often have very little lawn grass. B shows the total area which is represented by each fire frequency.*

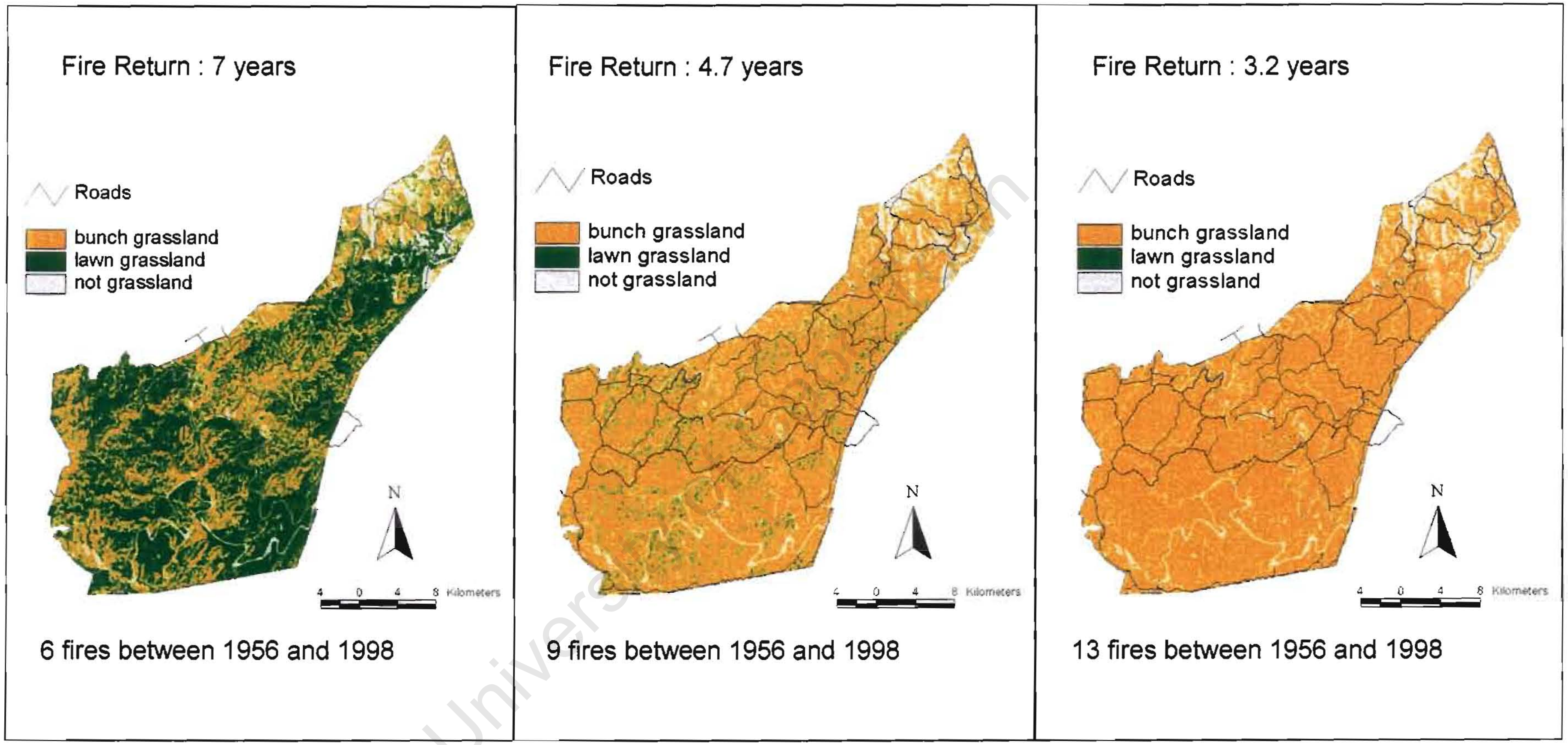

***Figure 6.5**: Potential distributions of lawn grass areas in Hluhluwe Umfolozi Park under 3 different fire frequency scenarios: The maps were created as back-predictions from a logistic regression model with fire history, slope, distance to water, and TRMI as significant determinants of grass community. These maps indicate that there are many areas of the park that could potentially support either grass community, and that fire history can alter the abundance of lawn grass areas considerably.*

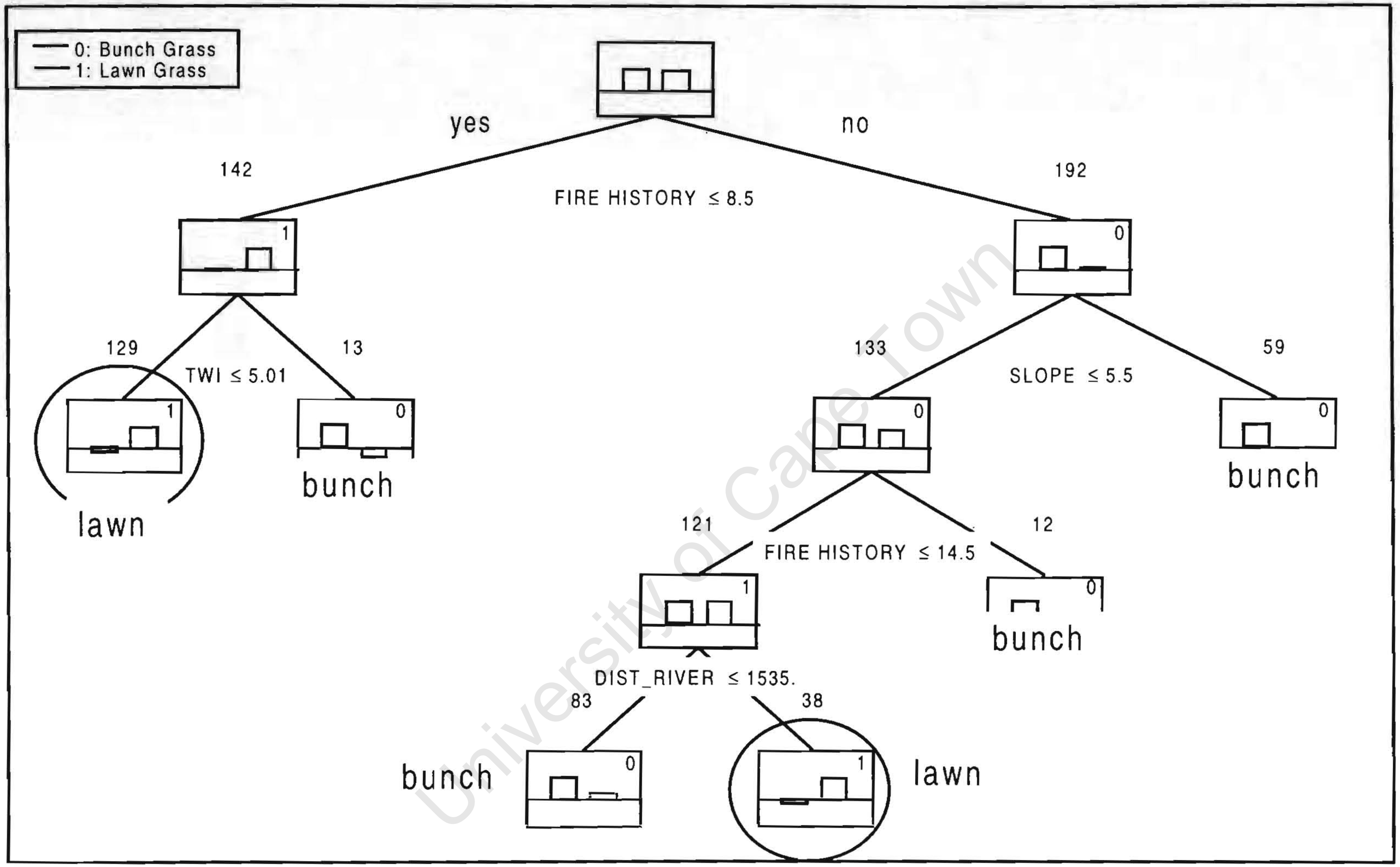

Figure 6.6: *Results of a non-parametric classification procedure run in STATISTICA. The initial sample is systematically classified into smaller categories based on the variables shown at each split. The bars in each box give an indication of the relative proportions of bunch grass (solid bars) and lawn grass (dotted bars) at each step in the procedure. When a bar is below the line it contains less than 5 samples. The numbers above the boxes represent the total number of samples which fell into that category. C&RT – style directive stopping, circled splits were classified as lawn grass.*

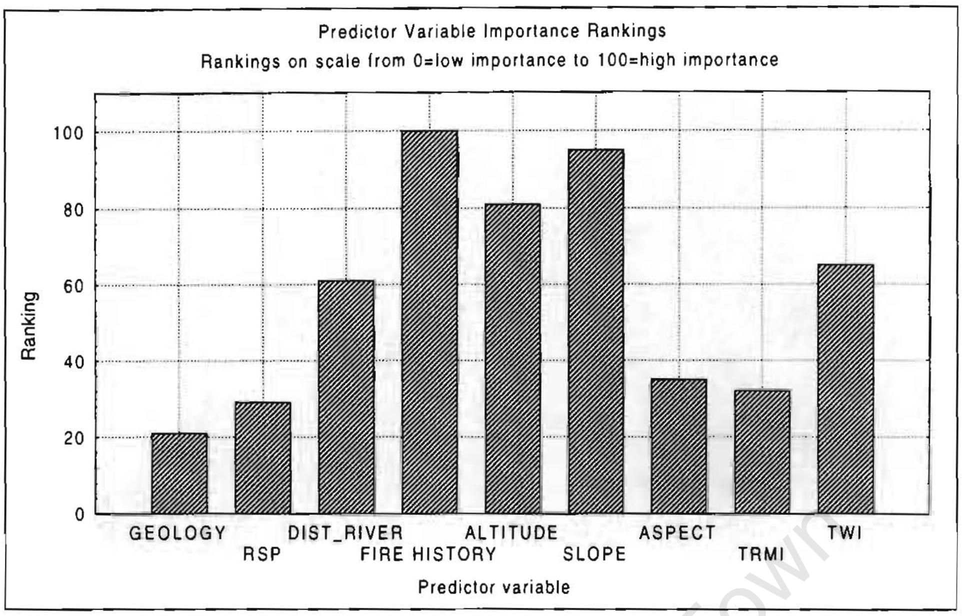

Figure 6.7: Ranking of predictor variables in order of importance in the classification tree (STATISTICA). Fire history and slope were also identified as the two most important predictors from the logistic regression (together with distance to river and the moisture index).

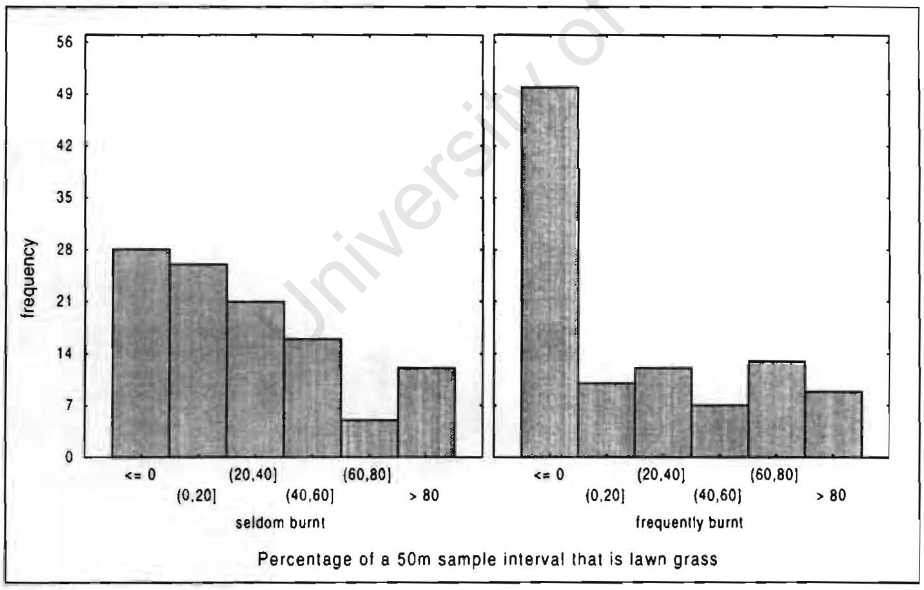

Figure 6.8: Histogram showing the distribution of lawn grass patch sizes on two comparable transects through frequently and infrequently burnt areas. Each 50m section of transect is classified as containing a certain proportion of lawn grass. The frequently burnt side had many sections with no lawn grass at all but there were patches of lawn grass in most of the sections on the seldom-burnt side. (Mann-Whitney U test z=2.33, p=0.019)

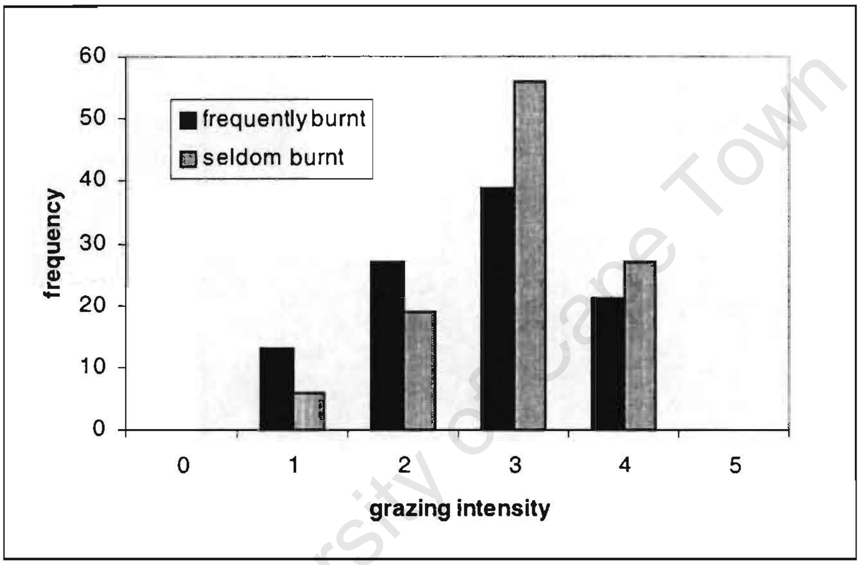

***Figure 6.9**: Frequency distribution of grazing intensity measures on two comparable transects through frequently and infrequently burnt areas. 0 = no grazing, 1=individual bites, 2=more unbitten than bitten, 3=more bitten than unbitten, 4=individuals unbitten.*

Discussion

This chapter presents evidence that fires have been affecting lawn grass proportions and distributions at HUP, and specifically that frequent fires are limiting lawn grass expansion.

In many savanna systems soils and rainfall are used to explain vegetation distribution (Scholes & Walker 1993). Water and nutrient availability will determine the vegetation, which can then also be affected by disturbances such as fire and herbivory. However, in this study soils and rainfall were not important factors in the regression models, and an analysis of lawn grass distribution in relation to geology showed no clear pattern. Grazing lawns were not found predominantly on one geological type and granite and basalt substrates, which might be expected to support more grazing lawns than sandstones, had no lawn grass areas at all. In this park, therefore, grass communities appear to be much more influenced by top-down control.

A regression between the proportion of grazing lawns and the frequency of burning in the last 42 years is highly significant (Figure 6.4A). With the exception of a few densely-forested areas (which have no grass) the less frequently an area is burnt the more lawn grass you are likely to find. The horizontal line in figure 4A indicates the overall proportion of lawn grass in the park: areas which have had less than about 10 fires have more lawn grass than average, while areas with greater than 10 fires have less lawn grass than average.

Implying cause from correlation is always problematic. The apparent correlation between fire frequency and lawn grass occurrence could be explained in various ways:

1. Lawn grass areas are less flammable, and therefore do not burn as readily (i.e. more lawn grass results in fewer fires, not that fewer fires result in more lawn grass). It is true that lawn grasses are generally shorter than bunch grasses, and that grass height affects fire spread. However, in this analysis the mapping of fire was done at a much larger scale than the mapping of grazing-lawn areas (management blocks of hundreds of Ha versus 32m pixels). When a management block is burnt the entire area is recorded as having burnt, even if the fire did not spread into the large grazing-lawn areas within the block. Therefore the correlation could not be explained by saying that lawn-grass areas prevent fires.

2. It is possible that managers burn blocks which have extensive lawn areas less frequently than they do bunch grass areas. This would also result in the correlation which we see. It is partially true that the decision to burn is often based on the perceived amount of flammable material (Balfour & Howison 2003), but fire policies have also been very variable over the period of study (since 1956). It is unlikely that any one fire management policy could have resulted in the clear pattern which appears.
3. The hypothesis as developed in this thesis - that frequent fires prevent lawn grass expansion by dispersing grazers - would also result in the correlation between fire frequency and grazing lawns. It is entirely consistent with the information on the effect of fire on grazing which is presented in Chapters 3 and 4. The long-term consequences of the interaction between fire and grazing would be the patterns of grazing lawn distributions which we see at Hluhluwe Umfolozi Park.

The multivariate analysis corroborates the regression results: fire history was the most important single predictor of lawn grass occurrence, and was included in all of the best multi-factor models (Table 6.3). As mentioned earlier, soil (geology) and rainfall (altitude) were not identified as important explanatory variables. One abiotic factor which *was* shown to be important was the index of soil moisture (Table 6.2, Figure 6.7). It is likely that where the soil is wetter, tall bunch grasses are at an advantage because they can grow taller faster (Huisman *et al.* 1999).

Other important variables - identified by both parametric, and non-parametric analyses - were slope and distance to permanent water, (Table 6.2, and Figure 6.7). These are both factors which are likely to affect grazing: areas further from water, and areas with very steep slopes are likely to be less heavily grazed.

Therefore, while there is evidence that site factors (soil moisture) can affect grazing lawn distribution at Hluhluwe Umfolozi Park, top-down controls, particularly the way in which grazing is mediated by fire frequency, appear to be more important. This is different from other wilderness areas in Southern Africa. In the Kruger National Park vegetation is clearly linked to soil-type, and at Nylsvlei grazing lawn areas are found predominantly in areas of duplex soils (Scholes & Walker 1993). It is possible that the complex pattern of soils and the hilly topography diminish the role that soils play in determining vegetation in my study area. Also, Hluhluwe Umfolozi Park has a very high grazer density compared to these other parks, and has particularly high numbers of white-rhinos – megaherbivores which have a disproportionate effect on vegetation (Owen-Smith 1988). Thus the importance of grazing in controlling vegetation is likely to be more obvious in this park than in other, less well-stocked reserves in the region. However, I do not think that the situation at HUP is unique: there are examples of grazer-controlled grazing-lawn systems in other reserves and rangeland situations in Southern Africa (Golden Gate National Park, communal areas in Kwa-Zulu Natal and Lesotho). This situation is likely to be found in any instance where grazer movements are influenced by fire, and will be mediated, but not eliminated by the effect of soils and rainfall.

This has some important implications for the effect of different fire policies on grazers, and on grazer habitat. Maps made from back-predictions from the logistic regression model are an indication of the variation in lawn grass distributions that could occur due to changed fire regimes alone. All other environmental predictors of lawn grassland were kept constant. The maps suggest that if the park was exposed to a much less intensive burning program (fire return interval of about 7 years), then much more of the park would become grazing-lawn habitat (Figure 6.5A). Grazing lawns are thought to have been more extensive in the park in the past (Bond *et al.* 2001), thus it should be possible to do some time-series analysis using older satellite images to see how realistic these maps are as predictors of lawn grass distributions.

The maps also predict that even a slight increase in fire frequency is likely to completely eradicate grazing lawns from the park (Figure 6.5B and 6.5C). If the entire park were exposed to the median fire frequency for the last 40 years then the proportion of lawn grass in the park is likely to drop to 6%. However, these predictions need to be viewed with the understanding that once large grazing lawn areas are established they are not quickly destroyed by a few years of frequent fires. Large grazing lawns are less affected by short term changes in grazing patterns, and even start to affect the spread of fires in their own right (Hobbs 1996). The regression model does not take this into account, and is therefore probably under-estimating the occurrence of grazing lawns at high fire frequencies.

The comparative road-transect gives descriptive data on how grazing lawns are affected by fire frequency. The frequently-burnt side did have some large grazing lawn areas, but these were extensive, permanent parts of the landscape that had probably been there long before 1956, which is when we start to have information on the fire history of the area. Thus it is not these permanent large patches, but the smaller patches (20-40m diameter), and the structure of the bunch grass sward, which give an indication of whether lawn grass patches are spreading or diminishing in the landscape.

About 50% of the frequently-burnt side of the road was homogeneous bunch grassland, with no lawn grass at all (Figure 6.8). Most of the sample intervals on the infrequently-burnt side of the road had <0 and <60% lawn grass. These would represent small lawn-grass patches, initiated by intensive grazing, which are maintained because fires have not been as influential on this side of the road. Present-day grazing is heavier on the patchy side, the side with infrequent fires (Figure 6.9).

In investigating the long-term effects of fire frequency on grass communities I have shown that:

- There are more grazing lawns in less-frequently burnt areas
- Fire history is an important predictor of lawn grass occurrence
- Areas which have had fewer fires have a less continuous grass sward with many small patches of lawn grass

However, I want to emphasise two points:

Firstly I did not have a no-fire situation to compare with. I was comparing different areas in the same park which had been exposed to different fire frequencies. However, as I made clear in previous chapters, the process that I am investigating is not localised in space: to some extent unburnt/infrequently burnt areas are still affected by nearby burnt/frequently burnt areas. There is some indication from Chapter 4 that the spatial extent of this effect is only a few kilometres, but I am not able to state conclusively that grazing in any part of the park has been unaffected by fires elsewhere. For this it would be necessary to find two comparable parks with different fire regimes over the last 50 years and that is not possible.

Secondly, in this chapter I have been concerned with the long-term effects of fire frequency on grazing and grazing lawns. However, I have not considered how other factors which vary in time could interact with fire frequency. As mentioned in the site description (Chapter 2), there is evidence that there have been large-scale fluctuations in grazer numbers in recent years, which would obviously affect the extent of grazing lawn habitats. Also, the periodic fluctuations in rainfall are likely to have a major impact on the grass sward: during periods of good rainfall the fast-growing bunch-grassland is likely to do well, and during periods of drought there is more chance that lawn grasses will be able to spread (Huisman *et al.* 1999). In fact, it is even possible that however intensively a bunch grass patch is grazed, lawn grasses will never establish properly unless the bunch grasses die out (due to drought or some other sort of disturbance). In the next chapter I discuss some of these interactive effects.

This work demonstrates a clear interaction between fire and herbivores as alternate top-down control agents influencing the nature of the ecosystem. If fires increase in a landscape, grazing lawn areas decrease, making the area less suitable for short-grass grazers. Once a system has become dominated by fire, and by the tall bunch-grasslands associated with fire, it is less likely that grazing-lawn habitats will spread. These processes are acting at a landscape level to shape the vegetation.

Chapter 7: Modelling the dynamics of grazing patches in relation to fire, rainfall and grazing at HUP

Introduction

The process that I have been investigating is a complex one, depending on subtle interactions between grazing, fire, and grass growth. Fires generally occur in August/September, at the beginning of the rainy season when grasses are just starting to grow and are most susceptible to grazing (Vallentine 1990). If short bunch grass is released from grazing at this time because of fires, and can grow fast enough during this period to become unpalatable, then there will be no incentive for grazers to return to the same patch, and the grazing patch will disappear. If, however, grazing is not significantly reduced by fires, or if rainfall is not heavy enough for the grass to grow tall and unpalatable, then the grazing patch will persist in the landscape.

Thus the current fire regime, rainfall and grazer density are all factors that could influence whether grazed patches persist in the landscape. It is likely that there will be certain conditions of rainfall or grazing intensity, where, whatever the fire regime, grazed patches will never last long enough to become permanent; and, conversely, some situations where patches will always remain short.

I was interested in the conditions favouring persistence of grazed patches and therefore the potential for lawn-grass expansion. HUP has been exposed to large-scale variations in fire regime and grazer numbers, and to periods of low and high rainfall (Chapter 2). To explore interactions between fire, rainfall, and grazer numbers and their effect on the expansion of lawn- vs. bunch-grass communities I developed a grid-based simulation model. Modelling was necessary because it is not possible to manipulate fire/fire size, rainfall or grazing density experimentally at HUP.

Rainfall

Patterns of animal utilisation of the grass sward are likely to be very different in dry and wet years; In dry years there is less forage available, and it is growing less vigorously, while in wet years there is much more forage, but the bunch grasses are also likely to grow much faster, and become tall and unpalatable faster. Presumably, dry periods are times when the bunch grasses are kept short for longer, and therefore times when lawn grasses would spread. It is likely that in wet periods, grazed patches would never persist' for longer than a season (growing faster than the animals can graze), whereas during drier periods even large fires would not act to destroy grazing patches.

Grazing

Bunch grasses grow very fast. Data from the ZLGP project records growth rates of 100-300g/month during the height of the growing season (see also van de Vijver 1999). In these tall-grass communities, grazing is what keeps grasses short. Thus grazing pressure needs to be very high to keep a patch of grass short during the growing season.

Fire

The impact of fire on grazers would be affected by the size of the burnt area: above a threshold fire size grazers would be dispersed off grazing patches, while below this threshold fire would concentrate grazers, creating areas of intensive grazing in the landscape.

Fire frequency would also be important in this process because it would control the amount of time that the patch is grazed before it grows up tall again (frequent fires= shorter grazing periods).

Methods

Basic design/model overview

I used a spatially explicit, grid-based, simulation model to investigate factors influencing the creation and persistence of short-grazed patches in the bunch-grass communities at Hluhluwe Umfolozi Park. Each cell represents a patch of grass of a certain height, and animals choose whether or not to graze cells based on the height of the grass in the cell. The initial landscape in the model is a uniform tall-grass sward, such as might be found in the park at the end of a wet growing season; grazed patches appear, spread, and disappear as the animals use the landscape, and as the grass grows throughout the year. A grazing unit is a 1x1m patch (roughly a quarter of the size of the smallest grazed patches found at HUP), and the extent of the simulation landscape is 25Ha (500x500 grid cells).

The resolution and extent of the model was constrained by the fact that I wanted to represent realistically how grazed patches develop – and thus needed to model foraging patterns at scales of at least 1m – but also to look at how these patches are affected by fire, which occurs at a landscape-level. Bunch grass areas cover most of HUP, and the fires that occur in these areas range from 500-3000Ha - too large an area for simulating the dynamics of grazing patches. Thus, conceptually, the 25Ha extent of my model represents a small portion of a much larger bunch grass landscape. The simulation landscape is always located at the edge of a burnt area in the larger landscape: when 25% of the entire landscape is burnt, then 25% of the simulation landscape is also burnt, if 5% of the entire landscape is burnt, 5% of the smaller landscape is also burnt (Figure 7.1). This means that the effect of landscape-level fires on grazing patterns in the simulation landscape reflects a process occurring throughout the park, and I can investigate the consequences of landscape-level fires at a non-landscape scale. Another advantage of this spatial scale is that there is no need to model the foraging movements of individual grazers, since all areas of the landscape would be equally accessible and visible to all grazers (see description of the grazing-module).

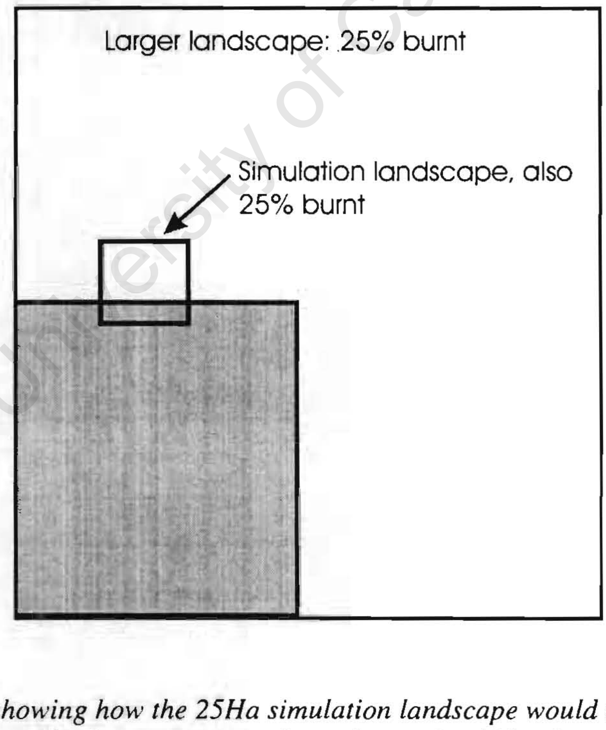

***Figure 7.1**: Diagram showing how the 25Ha simulation landscape would relate to a conceptual landscape of the entire park: the proportion of area burnt should be the same for both landscapes.*

The time step for the model is one month, and each simulation is run for a period of 10 years. 10 years is a long enough period of time for any contrived initial conditions to be eradicated, and to determine how dynamic grazed patches are from year to year; but short enough that there is no need to model grazer demographics, or to simulate the long-term periodic fluctuations in rainfall patterns that occur in this savanna system (Balfour & Howison 2003).

Model objectives

While the ultimate aim of the model is to investigate conditions under which lawn grasses can infiltrate a bunch-grass-dominated system, the competitive interactions between individual grass plants were not directly included. It is assumed that the longer the bunch grass remains short, the more likely it is that lawn grasses will be able to infiltrate (i.e. that bunch grass is only at a competitive advantage when it is tall and ungrazed). Thus my results are reported in terms of the persistence of grazed patches, and the proportions of the landscape that remain short; I am describing the competitive environment in which lawn and bunch grasses are interacting, rather than the interaction itself.

Variables considered

As mentioned in the introduction, the variables thought to determine the persistence of short grazed patches in the landscape were grazer numbers, rainfall, and fire frequency and size. Other variables, such as different grazer species, grazer diversity, and landscape (forage/soil/habitat) heterogeneity were kept constant in this simulation (Table 7.1).

Grazer numbers

At present the biomass of grazers is estimated to be about 90kg/Ha for the entire park (Data from HUP research station). I used three values of grazer numbers: present grazer density, double present, and half present (Table 7.1). Double present grazing numbers (c. 200kg/Ha) is similar to the stocking rate recorded on heavily stocked communal rangelands (Vetter, pers. comm.). Half of present grazing numbers (50kg/Ha) is close to the lower limit of the recommended stocking rate for commercial cattle farmers in this area (0.7 to 1.7 AU/Ha (or between 30 and 75kg/Ha) –Tainton 1999). The biomass of grass required by the grazers each month is calculated using an equation in (Owen-Smith 1988) on the dry mass required per day for grazers of different body-weights – see Table 7.1.

Table 7.1: Summary of parameters in model

	Parameter	Definition	Value
input variables	grazing_density	density of grazing mammals in the simulation landscape (kg/Ha)	400, 700, 1000
	rainfall period	prevailing rainfall conditions during the period of the simulation	dry, wet, average
	fire size	the percentage of the conceptual landscape (and also the simulation landscape) that is burnt each year.	0, 5, 10, 25, 50
	fire interval	number of years between fires	2,4, 6
constants	grazer species	species of grazer considered in model (affects palatable height and kg required each month	wildebeest
	palatable grass height	the maximum height (cm) of the grass considered as palatable by a specific grazer species	10
	short grass height	the height (cm) of the grass sward at which lawn grasses are able to infiltrate/compete with bunch grasses	5
	new patch probability	the probability (range 0.1-1.0) of the grazers initiating a new grazing patch in the landscape when there is no more palatable forage available	0.5
	minHt	minimum height (cm) to which the animals can graze the grass in a cell	1
model setup	cell size	landscape resolution: the size (m^2) of a grazing cell in the landscape	1
	landscape_dimentions	number of grazing cells on each side of the simulation landscape	500
	years run for	number of years that the simulation is run for under one set of conditions	10
calculated values	landscape_extent	size of the simulation landscape (Ha): (landscape_dimentions)^2*cell size/10 000	25
	kg_req	amount of grass required by grazers per month (kg dry weight)	kg_req per month = 30* tot_kganimals / [6*(kg individual animal) ^ (-0/191)*100]
	grass biomass	biomass of grass available in a cell of a certain height (kg dry weight)	biomass(grazing cell)= (0.014451*grsht(of cell)-0.025423)*cellsize
	grass_growth	height gain (cm) of grass in a cell over one month	growth_month1 = 1.52 - 0.1(grassHt_endMonth0) + 0.02(rainfall_month0)
	totPal	number of palatable cells in the simulation landscape	
	totAdj	number of unpalatable cells adjacent to palatable cells in the simulation landscape	
	cell_history	number of months that grass in a cell has remained below the short grass height	

*** all height values represent the height of grass measured with a light (100g) wooden disc dropped on the grass sward from a set height

Rainfall

I used rainfall data from Nqoyeni weather station in the centre of the park. The grass sward in this area is predominantly tall bunch grass. Rainfall data is available for this weather station since 1982.

To investigate how periods of below- and above-average rainfall affect the dynamics of grazing patches I created three different rainfall regimes, and ran each 10 year simulation under either dry, wet, or average rainfall conditions. These conditions were simulated using monthly rainfall data for 4 of the driest years (all with <600mm pa), 4 of the wettest years (>900mm pa), and 4 years of average rainfall (600-900mm pa). Each year, for a 10 year wet simulation, I would randomly pick one of the 4 wet rainfall years to input as monthly rainfall data; and similarly with dry, and average rainfall simulations.

Thus both sources of variation of rainfall in savannas (stochastic variation and long-term periodicity – Higgins *et al.* 2000) are included in the model; however, stochastic variation within a year is intrinsic to the model setup, whereas the influence of periodic variation in rainfall is investigated directly.

Fire Frequency

I used three different fire return intervals in the model: every 2 years, every 4 years and every 6 years. The mean, upper, and lower confidence limits for the park in the last 41 years are 4.4, 6.8 and 3.0 respectively (Data from Balfour & Howison 2002). The median fire frequency was only 1.3 years. Thus my values do not represent extreme fire frequencies for this system. If a fire occurred in a year this did not affect the probability that it could occur again the next year. This is realistic because in the mesic savanna system of Hhluhluwe Game Reserve the grass sward easily grows fast enough within one year to carry a fire again the next year.

Fire Size

The area of the park that burns each year has ranged from 0 to 800 000 Ha (90% of the park). In recent years there has been a general increase in the area burnt and at present between 30 and 50% of the park is burnt in any one year (Figure 7.2). I ran the simulation under 5 different categories of fire size: 0 (no fire situation), 5%, 10%, 25%, and 50% of the area

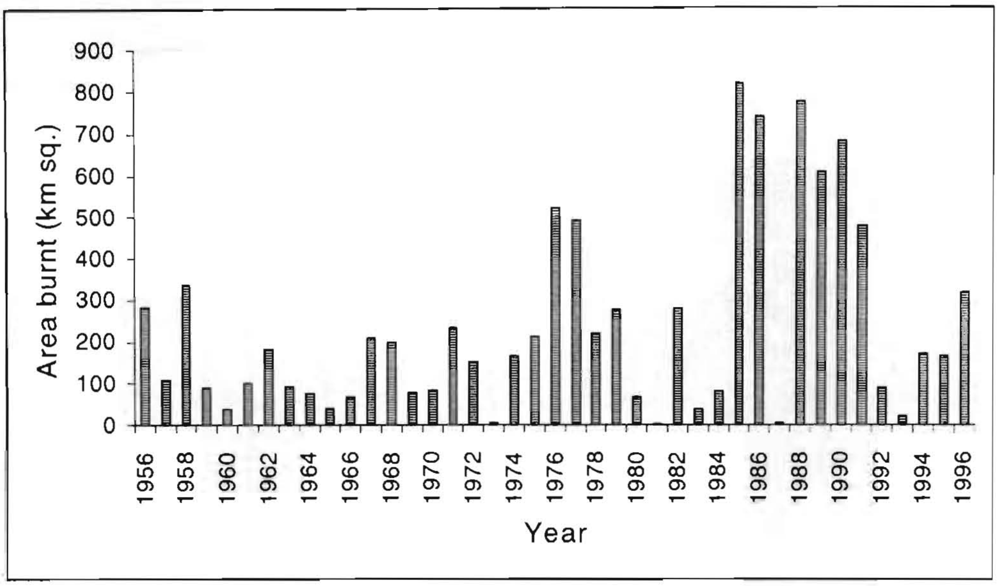

***Figure** 7.2: The annual area burnt (km^2) in Hluhluwe-Umfolozi Park for the period 1956 to 1996. Total area of park is 900km^2. Data from Balfour and Howison (2003).*

Simulation description

Each month grazing, fire, and growth occur sequentially: first, cells in the landscape are grazed based on a set of simple foraging rules; then, if conditions are right, fire can occur; then the amount of growth in each cell during that month is calculated. Figure 7.3 shows the flow of events during the simulation.

Grazing

A basic assumption of the model is that grass height is the main determinant of palatability: shorter grass is preferred to longer grass. This allowed me to simplify grazer foraging choices, because grass height is used as a comprehensive indicator of a range of forage quality parameters.

I believe that this is a valid assumption if one is considering a homogeneous grass community where species composition and soil nutrient concentrations are uniform in space. There is also evidence from the literature (Talbot & Talbot 1963; Lemaire *et al.* 2000) and from my experimental data (Chapter 4) that grazers select forage primarily based on grass height.

In the model, for a given grazer species, there is a grass height below which grass is palatable and preferred, and above which grass in unpalatable, and less preferred. Palatable height is likely to vary depending on the grazer (shorter for short-grass specialists), and on the grass species involved (species with low lignin content would

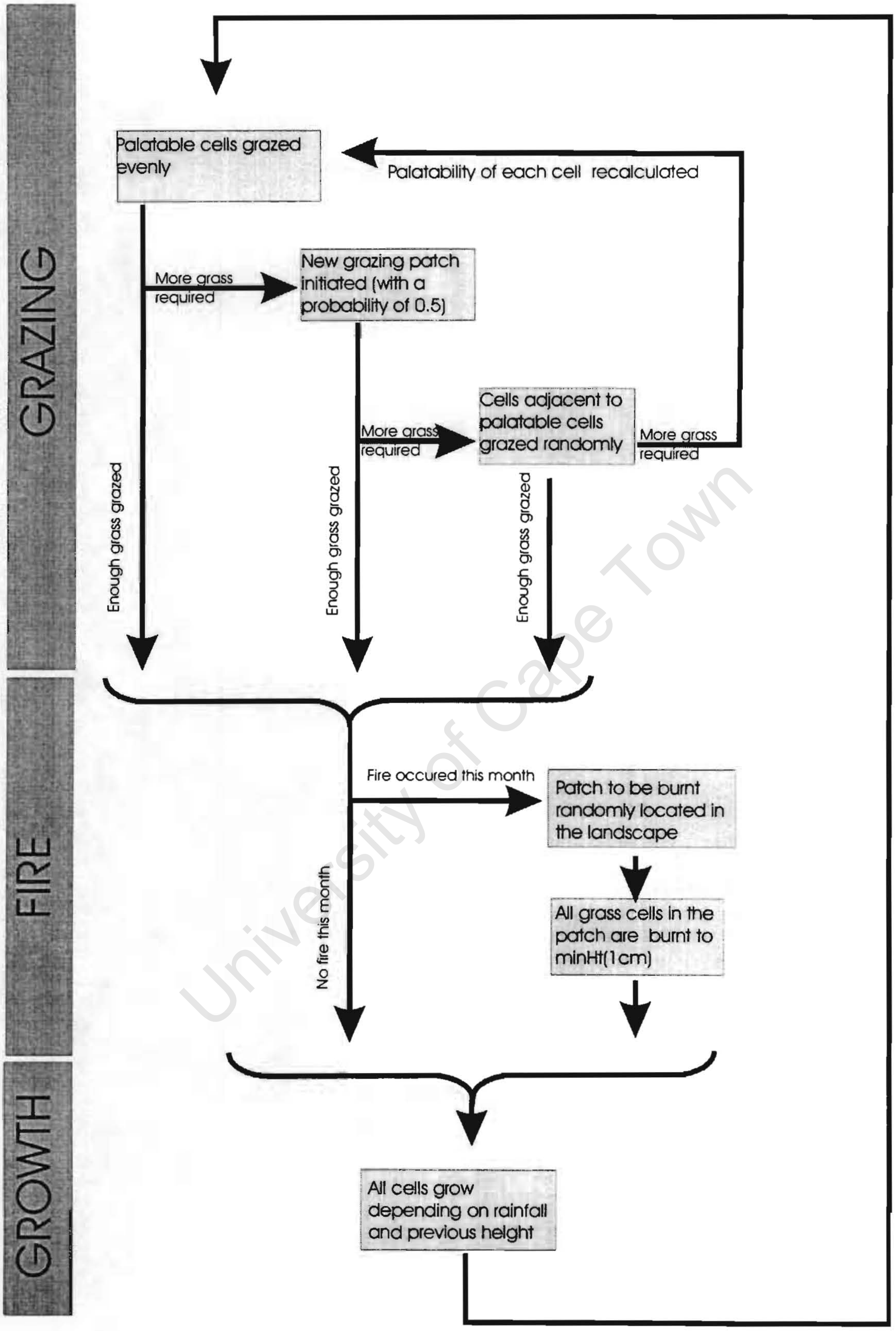

Figure 7.3*: Flow of events during one month of the simulation. Grazing occurs according to various rules, followed by fire if the conditions are right, and then finally growth.*

have a taller palatable height). In my model I minimised this variation by considering only one grazer species – wildebeest (for which I have empirical evidence of preferred grass height -Talbot & Talbot 1963) – and by simulating a very uniform grass layer with only one dominant species. The model could be altered to investigate the importance of grazer diversity/different types of grazers, and heterogeneity of soil resources/grass types.

To model foraging behaviour of grazers I assumed that all parts of the simulation landscape were accessible, and perceived by all grazers. Thus there was no need to simulate individual grazer choices. Also, within the time-frame of the model there was no change in grazer numbers – no demographic processes were included. Thus grazing pressure is set at the beginning of the simulation and remains constant throughout the simulation.

The amount of grass required by the grazers each month is determined from the grazer density (see Table 7.1), and the numbers of palatable, unpalatable, and adjacent-to-palatable cells in the landscape are calculated. Grazing then occurs in three steps (Figure 7.3):

1. Firstly all the available palatable cells are grazed evenly (i.e. the same amount of grass is eaten in all palatable cells).
2. Then, if still more grass is required, there is the possibility that the grazers initiate a new grazing patch. A new patch is created by grazing a randomly chosen unpalatable cell short. The probability of initiating a grazing patch is a predefined value between 0.1 and 1 (see Table 7.1).
3. If still more grass is required by the grazers, then they start to graze the unpalatable cells that are adjacent to the palatable cells – i.e. the unpalatable cells at the edge of a grazed patch are much more likely to be grazed than the rest of the unpalatable grass layer. An adjacent cell is selected at random, and is grazed to 66% of its original height (This value is used because Wade & Carvalho (2000)demonstrated in grazing trials with cattle that a single grazing event usually reduces the height of a grass sward by 33%).

Simulated grazing continues until either enough grass has been eaten to fulfil the needs of the animals, or there are no more adjacent cells. If there are no more adjacent cells and more grass is required then the process starts again: the numbers of palatable, unpalatable and adjacent cells are recalculated (based on the amount of grass biomass left – see Appendix 2) and the animals continue to graze.

Thus, within one month, the landscape can change from one of completely tall unpalatable grass, to one with a number of short grazed patches – enough to fulfil the grazing needs of the animals present. This is in line with what is seen in the reserve in the autumn. Animals start to move into uniformly tall bunch grass areas which can become studded with patches of short-grazed grass within the space of a few weeks.

One assumption that is inherent in this model is that the animals utilise the area all year round. Although the landscape represents only a small fraction of HUP (25 Ha), and although there is evidence that animals utilise the tall bunch-grass areas more during the dry season than the wet season (McNaughton 1983; Owen-Smith 1988), there is no movement into or out of the landscape. The consequences of this assumption will be discussed later.

Fire

Simulated fires occur in August – the most common time for management fires to occur (Balfour & Howison 2003). Each simulated year in August, the probability of a burn is calculated from the fire frequency (1:2, 1:4 and 1:6 probability of a fire respectively). When a fire occurs, a patch of predefined size (0, 5, 12, 25, or 50% of the landscape) is randomly located in the landscape. All parts of the landscape had an equal chance of being burnt in any one fire. The effect of a fire on a cell that burnt is to destroy all above-ground biomass by re-setting simulated grass height to the minimum possible grass height (1cm).

Growth

In the model, grazing and growth occur sequentially. The grass growth in a cell is dependent on two factors only: rainfall, and the initial height of the grass, i.e. shorter grass grows faster than taller grass. The grass growth function (Appendix 1) was derived from monthly height-gain data on 1 m plots protected from grazing at 17 different tall-grass sites in the park. The sites were cut short at the beginning of the season and height gain was measured monthly for one year.

Thus it is assumed that previous grazing history does not affect the rate of growth of a grass cell, that cells which have been grazed continuously for 10 years will grow as vigorously as cells which have only been grazed short once. This is known to be false. Previous grazing history decreases grass growth because it decreases stored reserves (Oesterheld & McNaughton 1991; Milchunas *et al.* 1995), and this means that any estimation of the persistence of grazed patches in the model landscape is likely to be conservative.

Assumptions made in the model

1. Grass height determines palatability.
2. There is a set grass height (for each grazer) above which grass becomes unpalatable and is not selected by grazers.
3. All parts of the landscape are equally visible and accessible to all grazers.
4. Grazing pressure does not change within a year, or between years (i.e. no demographic processes).
5. Palatable cells are grazed evenly.
6. Unpalatable cells next to palatable cells are much more likely to be grazed.
7. Animals utilise the area all year round – there is no seasonal movement into or out of the landscape.
8. Grass growth in a cell depends only on rainfall and initial grass height.
9. The amount of time that a grass cell remains short is an important factor affecting whether it is susceptible to invasion by lawn grass species. Grass community dynamics are not modelled, but the point of the model is to assess under which conditions more of the landscape is open to lawn-grass expansion. Thus the results that I report are based on this assumption.

Model calibration

I compared the amount of short-grazed patches created in the simulation landscape with empirical data collected on line transects through typical bunch-grass communities in the park. This data was collected in April of 2001 at the end of a year of above-average rainfall. The average percentage of the grass sward that was below palatable height (10cm) was 9%, but this is very variable: upper and lower 25% conf. limits 0% and 16% respectively. My model only predicts that 2.1% of the grass sward would be palatable (maximum 3.5%), and is therefore probably under-estimating the affect that grazers can have on the height structure of tall bunch grass.

The probability of initiating a new patch was a constant that required some sensitivity analysis. While this variable can have a big effect on the size and spatial distribution of grazed patches, it shows no predictable pattern with either average number of palatable cells, or the number of times that the grazed patches disappear. However, it does affect the proportion of the area that stays short (for values higher than 0.4 more of the landscape stays short). Therefore, for the purposes of this model, it was kept constant at 0.6.

Results

Figure 7.4 shows how the area that is grazed changes each month for the 10 year duration of the simulation under four different simulation conditions. In Figure 7.4A there is no fire, and, while the area grazed does fluctuate (increasing slightly during the dry season), it remains fairly high. When there is higher rainfall (Figure B) the average area grazed is less than in figure A, and the rainfall is sometimes so great that the grazed patches grow out, and new grazing areas have to be created and grow. When fires are a prominent part of the system (every 2 years on average – figures C and D), the area grazed fluctuates dramatically; being much increased after fires. This causes the grazed patches to disappear, and, as with figure B, new grazing areas have to be created often.

This pattern is shown in more detail in figure 7.5A, which summarises the number of times that grazed patches disappeared in the landscape under various conditions of fire frequency, rainfall, and grazing. Grazing does not seem to have much of an influence on patch persistence, but patches grow out much more often when there are frequent fires and high rainfall.

The size of fires does not show such a clear pattern (Figure 7.5B): with fire in the system patches disappear more often than they do when there are no fires at all, but this does not seem to be mediated by the size of the fires. Once again, high rainfall periods have a big impact on patch persistence, even in the absence of fire.

Figures 7.6(a-i) show how long different areas of the landscape are kept short during the 10 year simulation. Under high rainfall, and low grazing conditions – 7.6a – very little of the landscape remains short (98% of it was kept short for less than 1 year), and the frequency of fires does not affect this appreciably. However, under higher grazing conditions, more of the landscape is kept short for longer (in Figure c, 10% of it was kept short for between 1 – 4 years). It is only during lower rainfall periods however, that fire frequency starts to affect this pattern. In dry periods, with heavy grazing pressures (Figure i) then if fires are less frequent, more of the landscape will be kept short. Under a frequent fire regime no part of the landscape was kept short for longer than 4 years, but with less frequent fires 3-6% of the landscape remained short fairly permanently.

Figure 7.7A and B demonstrate these differences by comparing the percentage of the landscape that stays short for longer than 4 years under different fire, rainfall, and grazing conditions. Fire size never seems to have much of an impact, and it is only during average to below-average rainfall, and average to above-average grazing that fire frequency can be seen to have an affect. During high rainfall periods, or periods of very low grazing pressure, very little of the landscape remains short even without any fire in the system.

No interactive effect was found between fire size and fire frequency.

Figure 7.8 shows how fire size and fire frequency affect the amount of the landscape that stays grazed short for a long time. Frequent fires prevent any part of the landscape for being grazed for longer than a few years. When fires are infrequent fairly permanent grazed patches can develop. Small and large fires have a very similar impact on the grazing history of the landscape.

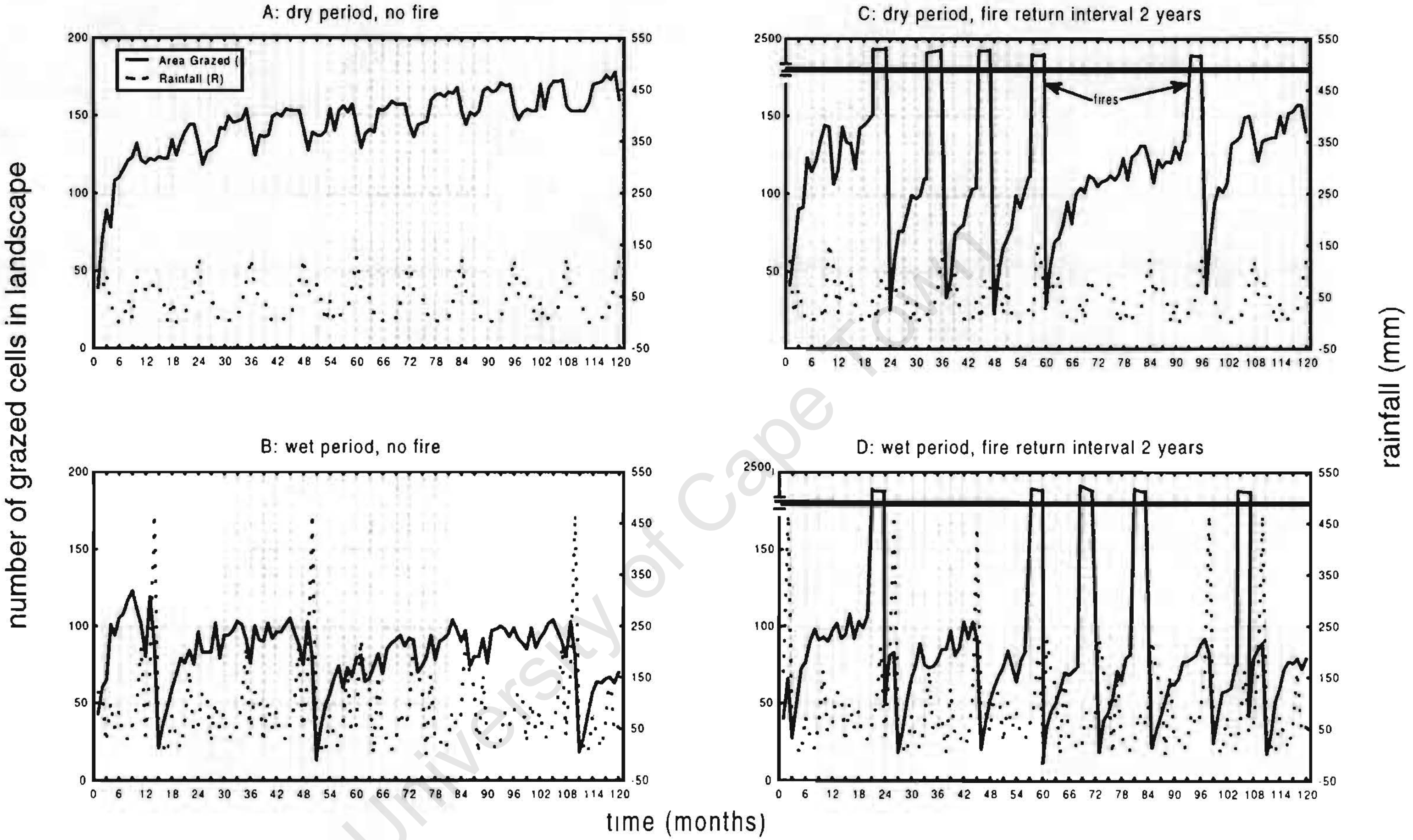

Figure 7.4: *Graphs showing how the area that is grazed changes each month for the 10 year duration of the simulation under four different simulation conditions. In figure A there is no fire, and area grazed remains high. In figure B the average area grazed is less than in figure A, and the rainfall is sometimes so great that the grazed patches grow out, and new grazing areas have to be created and grow. When fires are a prominent part of the system (every 2 years on average –figures C and D), the area grazed fluctuates dramatically; being much increased after fires. This causes the grazed patches to disappear, and, as with figure B, new grazing areas have to be created often. Thus, because high rainfall in itself can destroy grazing patches even in the absence of fire, fire does not change the patterns of grazing as much during wet periods as during dry periods. Grazer densities and fire size were kept constant at 50kg/Ha and 25% respectively for these simulations.*

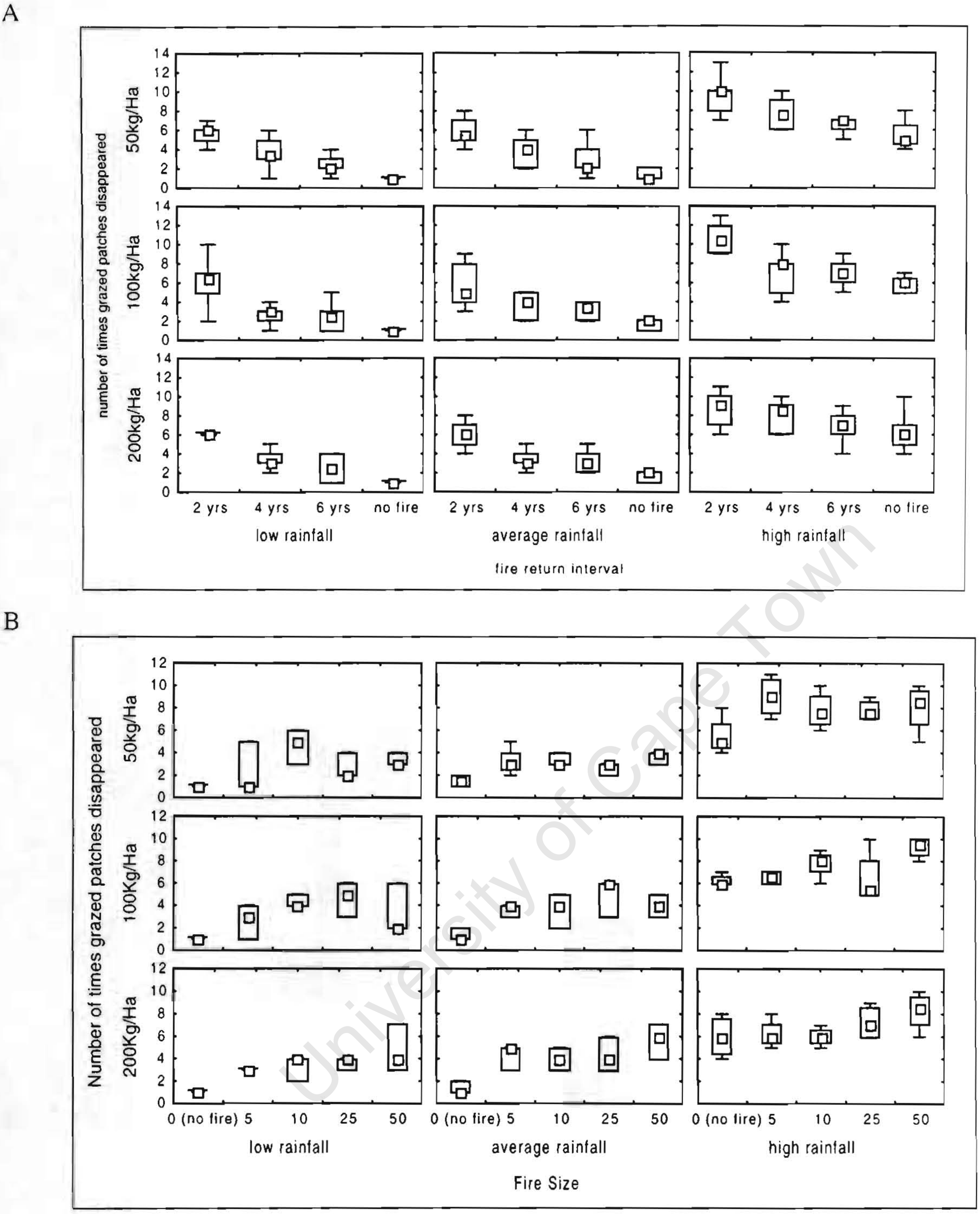

Figure 7.5: Showing how fire, rainfall and grazing affect the persistence of patches in the simulation landscape: Units are number of times that the grazed patches disappeared/grew tall during a 10 year simulation (Median and 75% conf. Limits). Rainfall on X-axis, Grazing density on Y-axis, and Fire return interval/fire size as box categories.
5A: Both fire return interval and rainfall influence the number of times that the grazed patches disappeared in the landscape: patches disappeared more often when there were more frequent fires, and when the rainfall was high. When there were no fires the grazed patches did not disappear unless the rainfall was very high. Grazing density does not seem to affect this process very much. Fire size was kept constant at 25% of the landscape.
5B: Fire size does not have a very clear impact on the persistence of grazed patches. It appears that fires of any size, will result in grazed patches disappearing more than they would under no fire conditions. Yet again rainfall has a big impact; during wet periods the grazed patches disappear very often and the effect of fire is possibly less important. Fire return interval was kept constant at 4 years.

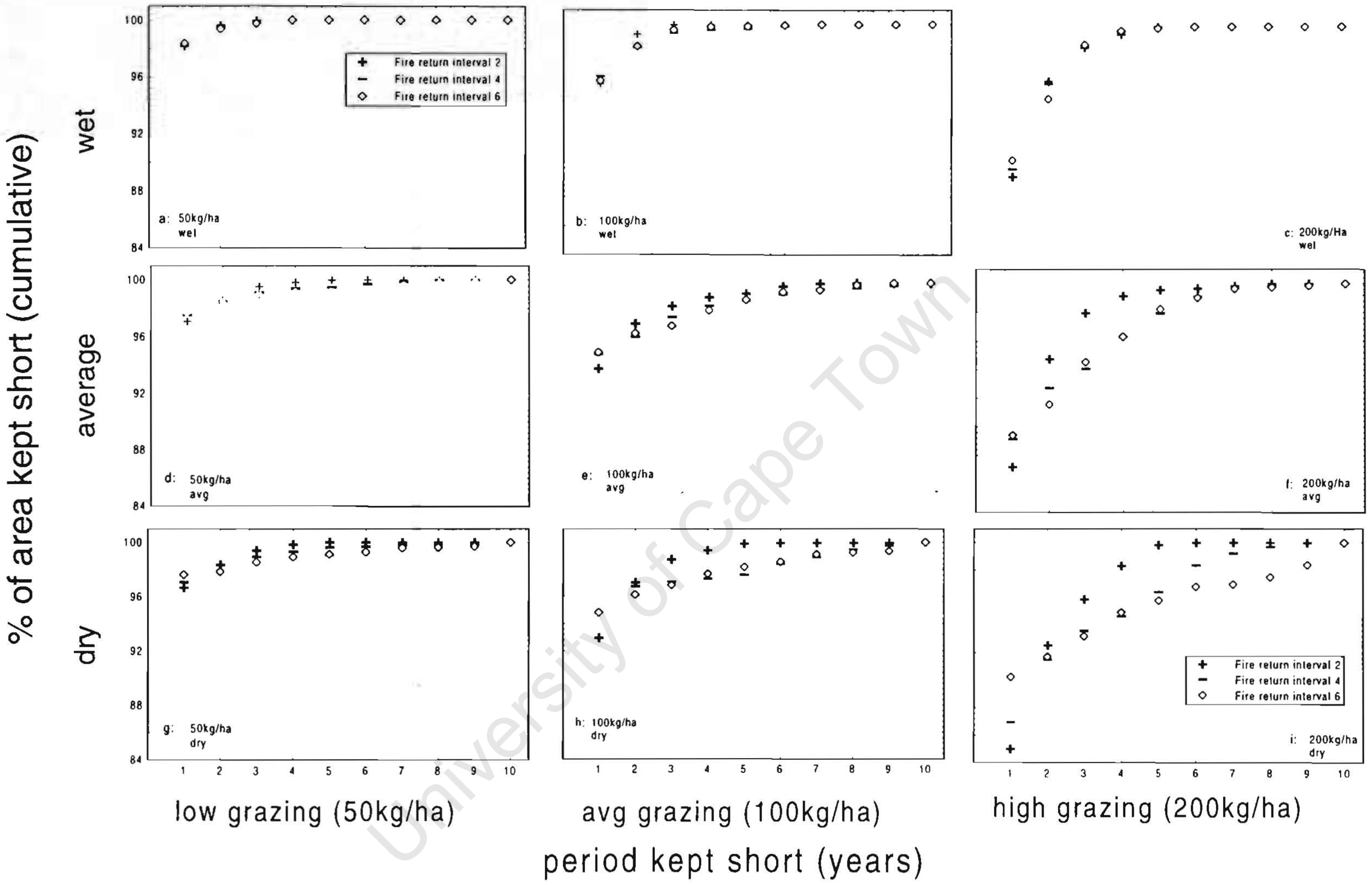

Figure 7.6: *Graph showing how long different areas of the landscape are kept short under different simulation conditions. Under high rainfall, and low grazing conditions (a), very little of the landscape is kept short (98% of it was kept short for less than 1 year), and the frequency of fires does not affect this appreciably. However, under higher grazing conditions, more of the landscape is kept short for longer (in fig c, 10% of it was kept short for between 1 – 4 years). It is only during lower rainfall periods however, that fire frequency starts to affect this pattern. In dry periods, under heavy grazing pressures (fig i) it is clear that if fires are less frequent (fire return intervals of 4 to 6 years) then more of the landscape will be kept short. Under a frequent fire regime no part of the landscape was kept short for longer than 4 years, but with less frequent fires 3-6% of the landscape remained short fairly permanently.* (these results are shown differently in figure7.7: which shows the average % of the landscape kept short for longer than 4 years under each simulation scenario.)

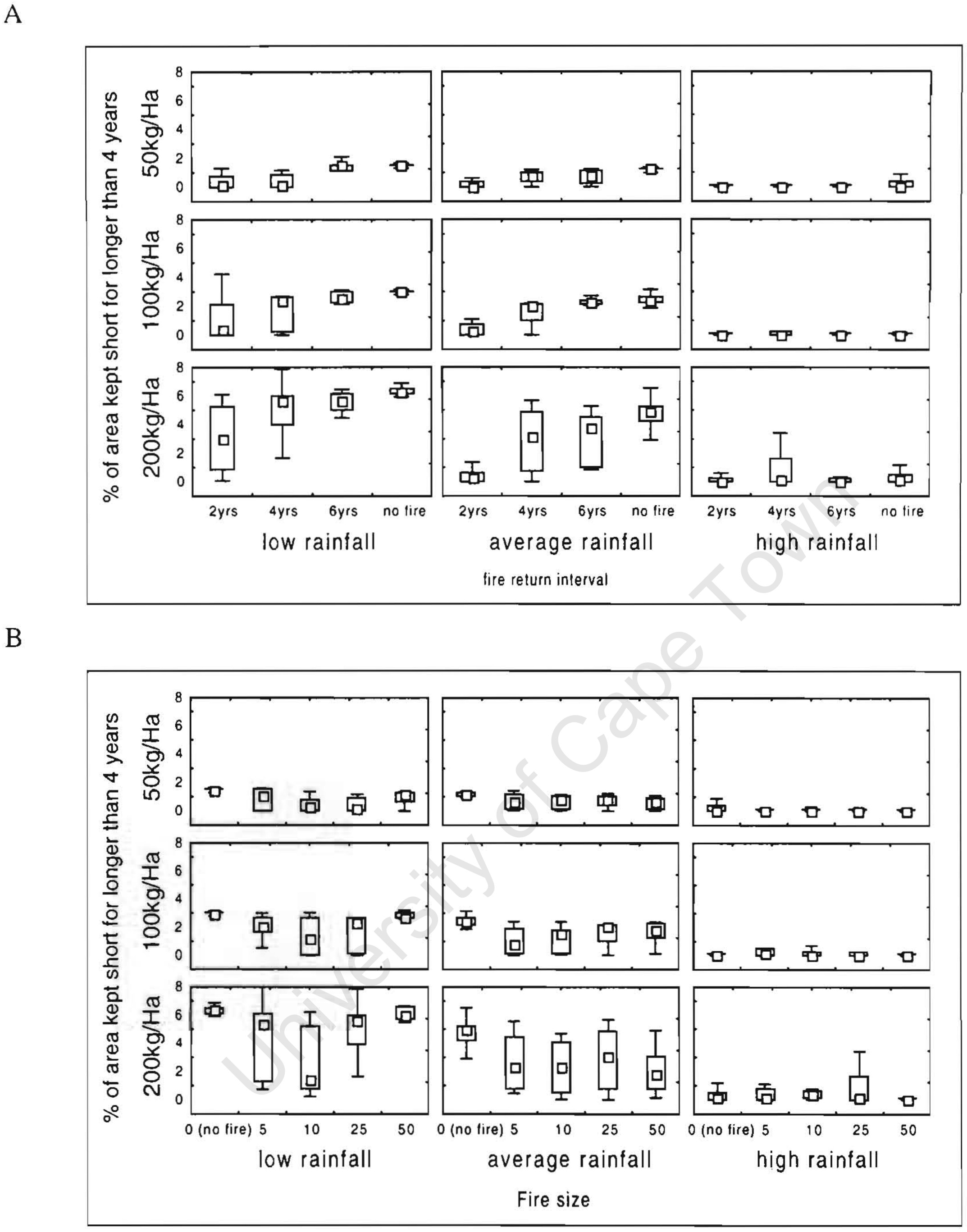

Figure 7.7: Showing how the percentage of the area that stays short for longer than 4 years is influenced by fire, rainfall and grazing densities in the simulation model. Rainfall on X-axis, Grazing density on Y-axis, and Fire return interval/fire size as box categories (Median and 75% conf. Limits).

A: Fire return interval has a much stronger effect during periods of low rainfall and high grazing
B: fire size does not seem to have a clear influence on the percentage of the area that is kept short.

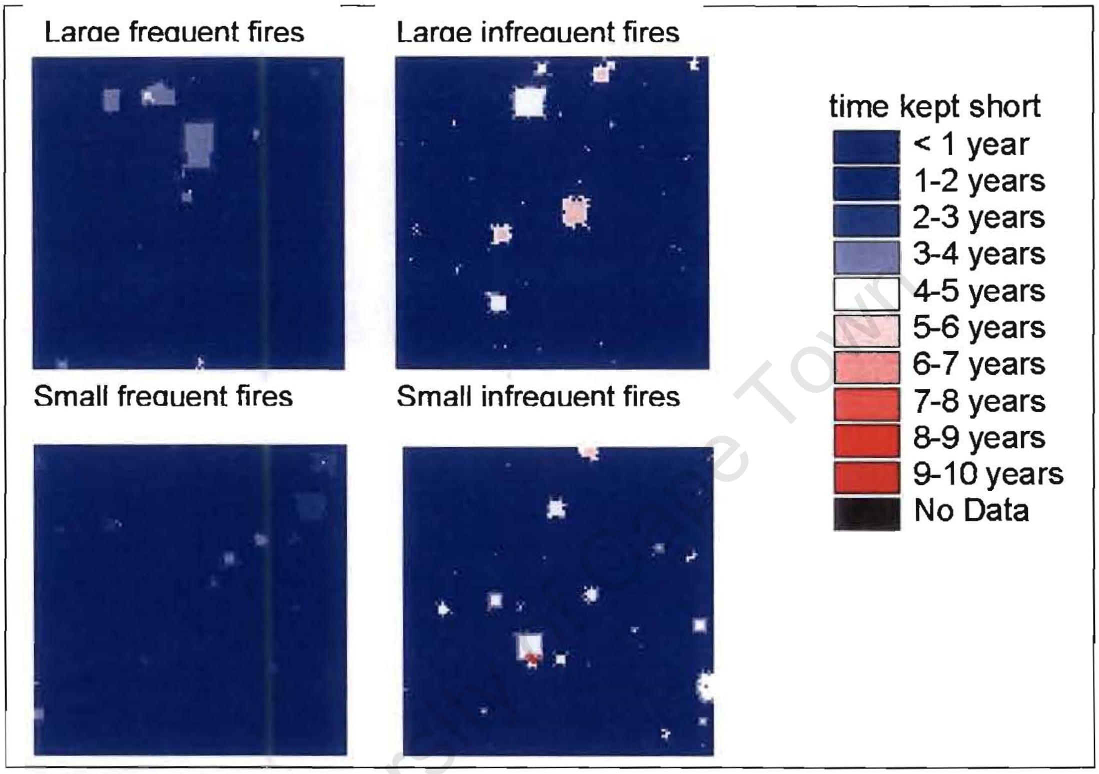

***Figure 7.8**: Showing the impact that fire size and fire frequency have on the grazing history of a landscape. Fairly permanent patches can develop when fires are less frequent, but fire size does not seem to affect this appreciably*

Discussion

In the simulation model the frequency of fires, mediated by rainfall and the density of grazers, can have an impact on the persistence of grazed patches in the landscape. Grazed patches disappear more often when fires are more frequent (Figure 7.5A), but for any given fire frequency, patches will disappear almost twice as often during periods of heavy rainfall.

Contrary to expectations, I did not find any clear pattern with fire size. Very small fires (5% of the landscape), had similar impacts to very large fires (50% of the landscape), both in terms of the number of times grazed patches disappeared, and the percentage of the landscape that remained grazed short during the simulation. Again, this was mediated by rainfall and grazer density, but more by rainfall than by grazer density.

Increasing fire frequencies have a very clear directional effect on both patch persistence and the amount of area that stays short. Even very infrequent fires (every 6 years) prevent patches from persisting as long as they would in the absence of fire. The simulation indicates that the effect of fire frequency on patch persistence is not linear: on average 3x as much grass stays short with a 4 year return interval compared with a 2 year interval, but only 1.3x as much for 6 versus 4 year return intervals. No interactive effect was found between fire frequency and fire size.

The model indicates very clearly that rainfall has a strong impact both on the persistence of grazed patches, and on whether fire frequency affects patch persistence. During periods of high rainfall, grazed patches do not persist in the landscape (Fig 7.5), and no part of the landscape remains short for very long (Figures 7.7). High rainfall alone can destroy grazing patches even in the absence of fire, so fire does not change the patterns of grazing as much during wet periods as during dry periods.

Grazing can also be seen to have an impact, especially on the amount of the area that stays short. As one would expect, at very low grazer densities even low rainfall and infrequent fires do not result in short grazed patches persisting in the landscape.

It is likely that grazer densities in the simulation landscape were never high enough for the effect of fire size to be apparent. In the absence of fire only about 3% of the landscape was grazed (see sensitivity analysis), so even very small fires (5% of the landscape) would be substantially increasing the total palatable area in the landscape. Fires would have to be very small to be acting as concentrating agents in this simulated system. Given that generally much more of the park than 5% is burnt in a year (Figure 7.2), my model predicts there would be very few years in which fire would be acting as a concentrating agent, creating grazed patches. However, this is not what is seen in the park. Sometimes, especially during periods of low rainfall, burnt areas do become the focus of next years grazing (as was seen in my experiment – Chapter 4). I think this is because, contrary to my assumptions in the model, not all of the landscape is equally visible, and equally accessible to grazers, therefore some burnt areas are likely to be preferentially used over others, and grazer densities in certain areas are going to be higher than the average for the entire park.

This simulation has given some indication of how important various interacting variables are in the persistence of grazing patches. Contrary to expectations, fire size did not affect how much of the landscape was kept grazed short. Nor did it interact with fire frequency in this regard. Fire size is more likely to influence spatial aspects of the process which were not investigated in this model. As would have been expected from empirical evidence in Chapter 6, infrequent fires did increase the amount of the landscape that stays short and the probability of a patch persisting. Grazer density, while important in itself in determining how much of the landscape is grazed, does not markedly mediate the effect of fire frequency. Rainfall, however, does influence whether fire frequency affects patch persistence, as well as affecting patch persistence in its own right.

If one accepts that fire and grazing can have the scale of effect demonstrated in Figure 5, Chapter 6, then it is important to understand them in the context of a highly dynamic savanna ecosystem. Understanding past changes in grass sward characteristics, and predicting future impacts of management strategies, depend on an understanding of how variations in fire, rainfall, and grazing can interact to effect these changes.

Appendix 1: *Calculating the grass growth function:*

Using STATISTICA general linear modelling module I ran a multiple regression with the dependent variable height gain, and the independent variables: previous grass height and rainfall. Data input were 113 records of monthly height gain at 17 sites over one season of growth.

Month and grass height were correlated (corr. Coeff. 0.71) and thus month was not directly included in the model.

The model was significant: $p< 0.01$ although the r-squared value was only 0.22 indicating that there was a great deal of variation that was not explained by the two independent variables. This is to be expected: the data was collected from sites with different grass communities, different soils, and different grazing histories, all of which are likely to affect height gain.

However, the residuals showed no pattern, and interactions between the independent variables and plot number were not significant, indicating that my results were unlikely to be confounded by other factors that vary with plot number. The fact that I used repeated measures of grass growth at the same site could be problematic, but month correlates with grass height – which is a dependent variable (Corr coeff = 0.71) – and thus, in a sense, is included in the model.

Thus the function used for grass growth in the model was:

Growth(month1) = 1.52 – 0.10(grassHt_endMonth0) + 0.02(rainfal_Month0)

This function returns slightly negative values at grass heights >30cm, which makes sense, as grass with this grass-height value is no longer actively growing taller, and old grass culms are decomposing and breaking down. Therefore, even when ungrazed, the grass in the model does not continue growing indefinitely.

Appendix 2: *Converting grass biomass to grass height*

There is a long tradition of using grass height as an indicator of grass biomass (Tainton 1999; Lemaire *et al.* 2000), and the relationship between grass height (measured by dropping a disc onto the grass sward from a set height) and grass biomass has been calculated for many grassland systems. At HUP the relationship was calculated using 200 measures of grass height and grass biomass, which were collected throughout the season and over a range of grass communities (ZLGP data). The relationship is significant at $p<0.001$, and the r^2 value is 0.64:

Grass biomass(kg/m2)=(144.51*veght(cm)-254.23)/10 000

Therefore, in the model,
The biomass of grass in a grid cell= (0.014451*grsht(of cell)-0.025423)*cellsize (Table 7.1)

Chapter 8: Conclusion

The research presented in this thesis is significant because it investigates mechanisms and processes occurring at a large spatial scale. Previous work on spatial aspects of fire regimes has been mainly descriptive, dealing with how different fire sizes and frequencies create or destroy heterogeneity (Briggs *et al.* 1998; Brockett 2001). However, in this example fires are affecting the landscape not only directly – altering vegetation structure – but also indirectly, by influencing the way that another important control agent, grazing, functions. Dynamics at a localised site are dependent on the much larger spatial context of the distributions of burns in the landscape.

I have shown that fire and grazing are interacting to produce complex patch dynamics in the grass layer. By controlling where, when, and for how long, animals graze a patch, fire is controlling rates of regrowth and influencing the competitive balance between grazing-tolerant, and grazing-intolerant grass species. The long-term effects of this interaction can be shown to influence the proportion and distributions of different grassland habitats in the landscape (Chapter 6).

Therefore fires and grazing can be seen as two competing forces. Under conditions where fires are large and frequent the landscape is dominated by grasses promoted by this disturbance. Fire-prone, tall, bunch-grass species clothe the landscape, together with the animals and trees that are adapted to this environment. This situation is self-maintaining because the more fire there is in the system, the more these grass communities will spread. Similarly where grazing dominates the system, and fires are less common, grazer-adapted grass communities, and their associated fauna and flora, become more extensive. This is also likely to be a self-maintaining process because grazing can reduce fire spread. Savanna landscapes are being fashioned by a power play between influential, but often antagonistic forces acting in a complex spatial environment.

It is not surprising that these sorts of processes have remained unrecognised in savanna and grassland systems. Most areas the world have a highly depauperate large mammalian fauna (Owen-Smith 1989; Flannery 1994). Thus in most savanna systems fire-landscapes seem to have won by default – as the grazers died out fires would have become larger and more frequent (Flannery 1994). The interactive processes between top-down control agents would have been lost to the system. Africa is the only continent with a recognised grazing-lawn grass community; stoloniferous grasses are a very small, ecologically insignificant component of most other systems. It is possible that these grass communities were prominent on other continents in the past, but died out with the grazers as fires spread in the landscape (Mack & Thompson 1982).

Thus it is only in Africa that it is possible to investigate the ecosystem consequences of such a fire-grazing interaction. How important is this process in the context of other controllers of vegetation distribution? And how can we, as self-proclaimed managers of our ecosystems, use our understanding of this process to influence the landscapes of nature reserves and wildlife areas?

These questions are yet to be answered. We do not yet know what range of grass communities could be represented in different savanna/grassland ecosystems, given that there are always constraints imposed by the abiotic conditions. The modelling work (Chapter 7) and the logistic regression model (Chapter 6) suggest that in mesic systems the fire-grazing interaction will be less important: the persistence of grazed patches would be controlled more by rainfall. The situation at Hluhluwe Umfolozi Park implies that soils are less important than previously thought, and that grazing-lawn communities can occur on many different substrates, depending on the history of fire and grazing. It is not clear how this translates to other parks where vegetation is more strongly linked to soil properties.

However, I suggest that there *are* savanna systems whose abiotic characteristics could support both lawn- and bunch-grass communities. Which community type is dominant would therefore depend on grazing, rainfall, and fire history. At Hluhluwe Umfolozi Park there is evidence of large-scale changes in grass community distributions over time although it is not easy to infer causal relationships.

Management implications of this are debatable. Farmers use fire to influence cattle grazing in unfenced rangelands in South America (Geldenhuys pers comm.). These farmers light frequent, small fires to enforce a system of rotational grazing. Fuhlendorf & Engle (2001)advocate the use of fire to create a patchwork of areas that are grazed with varying intensity and frequency.

In National Parks in Southern Africa fire management is a complicated process. It has many different, often competing, goals. It is used to control tree densities, combat ticks, manipulate the grazing resource at key times of year, as well as to control other fires. It is now also being used to affect patch dynamics and vegetation structure so as to create optimum habitat for small mammals, birds and insects, (Brockett 2001; Allan & Southgate 2002). Perhaps it is too much to expect managers also to be thinking of the long-term consequences of fire regimes on grass communities. However, it is important to realise that a management strategy of frequent large fires, which is often justified as providing food for grazers, could in fact be doing exactly the opposite and decreasing the extent of grazer-preferred lawn-grass areas.

Results from the model (Chapter 7) suggest that it is during times of drought that fire is most influential in affecting grazing-patch persistence. The drought of the 1980s showed us that grass communities are remarkably resilient and grow back rapidly when rains start again (Walker *et al.* 1987). Therefore, management decisions during droughts can take considerations other than the short-term impacts on the grass resource into account. These periods could be seen as an opportunity to shape the environment of the park for the next wet period, as an opportunity to influence the proportions of different habitat types and the environment that grazers are going to be inhabiting for many years to come.

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