Spatial and temporal variability in *Acacia* population dynamics

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Abstract

Variability in fire, herbivory, and climate facilitate the coexistence of trees and grasses in savannas and impact upon savanna structure, which also varies substantially both spatially and temporally. These features can shape savannas at an ecosystem and even at a global scale, but mechanisms for the effects of fire, herbivory, and climate variability on tree cover are often demographic at the tree population level. Sapling growth in particular has repeatedly been shown to be the limiting step, or 'bottleneck', in the establishment of trees in savannas. I set out to investigate how spatial and temporal variability in fire, herbivory, and climate shape population dynamics of a suite of common African savanna trees, the *Acacia*, in a landscape context. I carried out my field work in Hluhluwe iMfolozi Park in KwaZulu Natal, South Africa, during 2006 and 2007.

Fire, herbivory, and the grass layer were primary determinants of distributions and co-occurrence of *Acacia* species. They primarily affected saplings, indicating that sapling survival may determine distributions of adults. Moreover, communities were structured by species' direct interactions with fire and herbivory, rather than by competitive interactions with each other. Spatial heterogeneity in fire and herbivory resulted in an ecologically diverse suite of *Acacia* species.

Even within the environments in which different species occurred, both fire and herbivory had the ability to directly suppress *Acacia* sapling growth and limit establishment of adult trees. Sapling growth and maturation, rather than seedling establishment or sapling mortality, appeared to be the limiting step. A herbivore exclusion experiment showed that at mesic sites, where growth rates were higher, browsing and fire acted together to limit sapling growth, while at semi-arid sites, browsing or fire alone was sufficient to prevent saplings growing. Reductions in browsing resulted in increases in sapling growth, indicating that variability in herbivore pressure impacts adult establishment and tree population dynamics.

A long-term study of establishment of *Acacia* trees using age estimation of adults via dendrochronology indicated that tree recruitment is not continuous at local or landscape scales. *A. karroo* recruitment occurred within the last 20 years during periods without fire on a local scale; however, on a landscape scale, decreases in fire frequency were linked to periods of drought. I was unable to link recruitment of *A. nilotica* and *A. nigrescens* directly to climate, fire or herbivore population records, but recruitment of both species appeared to have stopped in the 1970s. In mesic areas, dominance seemed to be shifting from *A. nilotica* to *A. karroo*, while in semi-arid areas, large *A. nigrescens* trees are not being replaced. This suggests that major shifts in species dominance and even savanna structure are characteristic of these savannas.

Savannas are highly variable systems that are not adequately described by equilibrium ecology models. Non-equilibrium dynamics must form a more fundamental part both of theoretical savanna ecology and of savanna management.

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Chapter 6: Continuous versus episodic recruitment in three African *Acacia* species............................(con't.)

Chapter 1

General Introduction

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Chapter 1 - General Introduction

Savanna is defined by having a continuous grass layer and with a discontinuous tree layer and is among the most globally widespread biomes. Although rainfall and soils are considered key determinants of savanna distribution and structure (Scholes & Archer 1997), savannas occur in diverse areas of high and low rainfall and of variable soil fertility, making them difficult to define on the basis of climatic and edaphic processes alone. Even so, the dominant paradigm for understanding the coexistence of trees and grasses in savannas describes trees and grasses sourcing water from different niches. The Walter hypothesis suggests that trees source water from deeper soil horizons and grasses source more ephemeral water from shallower soil horizons, resulting in potentially stable, equilibrium tree-grass coexistence described by Lotka-Volterra competition (Walter 1971; Walker & Noy-Meir 1982). Recent syntheses have suggested that the Walter hypothesis is not a universal or ubiquitous driver for tree-grass coexistence in savannas (Scholes & Archer 1997). In fact, the trees and grasses in savannas may not be described by stable coexistence at all (e.g. Higgins *et al.* 2000). Tree-grass ratios fluctuate much more widely than equilibrium concepts allow, even over relatively short time periods (Walker *et al.* 1981; Westoby *et al.* 1989; Gillson 2004). Moreover, this root niche-differentiation hypothesis offers no good explanation for why woody biomass is often substantially less than the 'climate potential' for savannas around the world (Bond 2005; Bond *et al.* 2005; Sankaran *et al.* 2005).

Savannas are probably not equilibrium systems, but defining non-equilibrium, especially as a useful concept for management and applied ecology, is a challenge (Ellis & Swift 1988; Illius & O'Connor 1999; Sullivan & Rohde 2002). Elucidating the drivers, processes, and mechanisms that define savanna structure and make savannas variable, non-equilibrium systems without a clear 'climax' state is necessary for translating non-equilibrium concepts into practical and applicable management principles, for rangelands and conservation areas alike.

Fire, herbivory, and even rainfall are among the variable features in savanna systems that are widely considered to be drivers of savanna structure (Skarpe 1992; Scholes & Archer 1997; Sankaran *et al.* 2004). Fire has been shown to suppress tree cover below its theoretical 'climate maximum' in savannas worldwide (Bond 2005; Bond *et al.* 2005; Sankaran *et al.* 2005), and herbivory can prevent tree recruitment in systems with extant native herbivore assemblages (Prins & van der Jeugd 1993; Barnes 2001; Augustine & McNaughton 2004). Nonetheless, trees do establish under conditions that often do not favor them. Multiple authors have suggested that fire (Hoffmann 1999; Higgins *et al.* 2000) and herbivory (Belsky 1984; Prins & van der Jeugd 1993; Barnes 2001) limit tree establishment by suppressing growth of saplings and preventing them from recruiting into adult trees. Saplings persist under conditions of frequent fire or intense browsing until they are able to escape or are released and recruit into adults (Prins & van der Jeugd 1993; Higgins *et al.* 2000). Herbivore effects are somewhat more difficult to generalize; browsers and grazers have distinct effects on savanna vegetation. Browsers can directly suppress sapling growth (Belsky 1984; Barnes 2001; Augustine & McNaughton 2004; Sharam *et al.* 2006), while grazers can facilitate tree establishment, primarily by reducing grass biomass, resulting in decreased fire frequency and intensity (Sharp & Whittaker 2003; van Langevelde *et al.* 2003; Archibald *et al.* 2005; Collins & Smith 2006) and decreased grass competition (Walter 1971; Walker & Noy-Meir 1982; Madany & West 1983).

Climate variability may also fundamentally shape savanna dynamics. In arid savannas, seedling establishment has repeatedly been shown to occur primarily in years with exceptionally high rainfall (O'Connor 1995; Watson *et al.* 1997; Wiegand *et al.* 1999; Wiegand *et al.* 2004), resulting in even-aged cohorts of trees. However, the extent to which episodic seedling establishment is important in savannas is unknown, and in many cases episodic seedling establishment does not dominate tree population dynamics, although seedling establishment can still be discontinuous (Watson *et al.* 1997; Wiegand *et al.* 1999; Wiegand *et al.* 2004). Rainfall can also impact on tree demography in savannas by influencing fire and herbivory dynamics in the landscape. In both mesic and semi-arid savannas, interannual rainfall variability determines grass growth, fuel loads, and fire intensity (Scholes & Archer 1997; Higgins *et al.* 2000; Balfour & Howison 2001; Knapp *et al.* 2001). Tree growth can also depend strongly on rainfall (Miller *et al.* 2001), which could influence rates of adult establishment or probability of 'escape' from the effects of fire and herbivory.

Temporal variability in fire, herbivory and rainfall are probably major features affecting tree populations and especially tree establishment in savannas. However, savanna landscapes are spatially heterogeneous as well, and fire and herbivory in particular are spatially variable (Urban *et al.* 1987; Coughenour 1991; Bailey *et al.* 1996; Schwinning & Parsons 1999; Heyerdahl *et al.* 2001). Considering spatial variability is an important component of understanding how rainfall, fire, and herbivory play out in savanna landscapes. Scale matters; hierarchical patch dynamics suggest that dynamic heterogeneity at a local scales aggregates, resulting in stability at a regional scale, constrained by climate. Thus, the scale of observation can determine what processes shape savannas (Coughenour & Ellis 1993; Gillson 2004). Climate often governs species distributions and savanna structure at continental and regional scales (Williams *et al.* 1996; Scholes *et al.* 2002; Gillson 2004), but even at the continental scale, determinants of savanna distribution and non-equilibrium savanna dynamics are under debate. Fire has a substantial role in determining global savanna distribution (Bond *et al.* 2005; Sankaran *et al.* 2005), although both fire and herbivory are usually considered to be important more locally (Eckhardt *et al.* 2000; Moreira 2000; du Toit 2003; van Wilgen *et al.* 2003; D'Odorico *et al.* 2006). Multiscale non-equilibrium is relatively new to savannas. Spatial and temporal dynamics of savanna structure are largely unknown, and the relationship of these patterns to a dynamic set of drivers is an open question.

This thesis investigates the effects of temporal and spatial variability in rainfall, fire and herbivory on aspects of the demography of common species of *Acacia* in Hluhluwe iMfolozi Park in KwaZulu Natal, South Africa (for a description of study site and its history, see Chapter 2). Questions central to the four data chapters as follows:

Chapter 3

- Fire, herbivory, and the grass layer are spatially heterogeneous in savannas
- Do fire, herbivory, and grass determine tree species distributions and govern tree community assembly?
    - Neutral vs. niche community assembly

Chapter 4

- Herbivory is a variable feature of savannas, but does it impact on seedlings and saplings?
- Are effects localized in areas of intense herbivory? Is herbivory only important at a local scale, or can herbivores impact a whole landscape?

Chapter 5

- Establish a method using tree ring counts and radiocarbon dating for ageing trees for Chapter 6

Chapter 6

- Temporal variability in tree recruitment
- Is tree recruitment continuous, consistent with 'equilibrium' savanna models?
- If recruitment is not continuous:
    - Is variable recruitment related to special conditions or events from rainfall, herbivore population, and fire records?
    - Are patterns in variability different from local to landscape scales?

Chapters 3 through 6 have been prepared as stand-alone papers. Each chapter has a theoretical introduction that includes ideas discussed in this introduction and in other chapters, resulting in some repetition. Chapter 2 provides background on the study site. Chapter 7 synthesizes conclusions and implications. I did data analysis and write-ups of all chapters and data collection for all chapters except for Chapter 3. For Chapter 3, I have listed as authors people who did data collection. For other chapters, I have listed as authors my supervisors, whose intellectual contribution to this work was substantial.

Chapter 2

Study Site

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Chapter 2 – Study Site

This thesis hopes to examine changes in the tree layer in Hluhluwe iMfolozi Park in relation to variable climate, fire frequency and intensity, and herbivore pressure. Background information on the geology, climate and vegetation of the Hluhluwe iMfolozi Park landscape and a clear understanding of how fire management and herbivore population and landscape management have changed throughout the history of the park are vital to interpreting changes in the tree demographies.

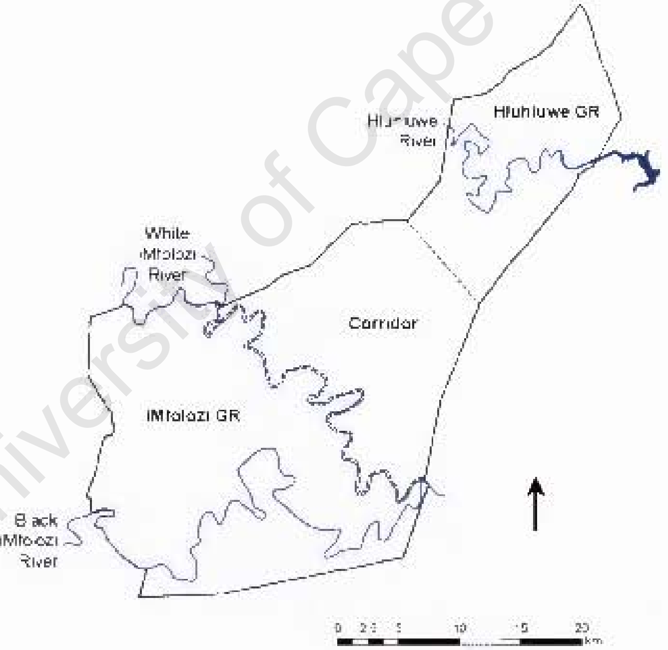

Figure 2.1. Map of Hluhluwe iMfolozi Park with management sections and major rivers. Hluhluwe and iMfolozi Game Reserves were declared independently in 1895. Although the corridor area was administered as Crown Land and only officially incorporated into the reserve in 1982, the Hluhluwe iMfolozi Park complex was fenced as a whole in 1963.

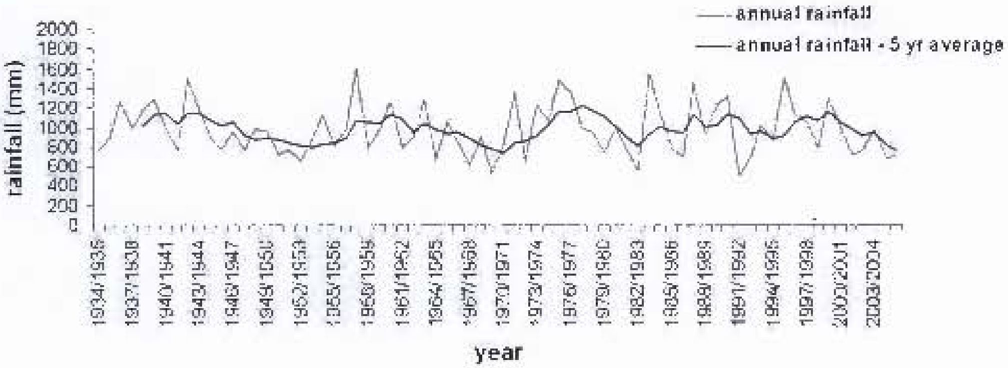

Figure 2.2. Annual rainfall at Hilltop Camp in Hluhluwe Game Reserve.

All work for this thesis was conducted in Hluhluwe iMfolozi Park (28°00' – 28°26' S; 31°43' – 32°09' E), located in northern KwaZulu Natal, in eastern South Africa, and covering an area of approximately 89,000 ha (see Figure 2.1). Topography is varied, consisting mainly of rolling hills of up to 540m elevation in the Hluhluwe Game Reserve area falling into broader river valleys at 40m elevation in the iMfolozi Game Reserve area. Soil types are closely linked to bedrock geology (Graham 1992), consisting predominantly of shales and sandstones with intermittent doleritic intrusions (King 1970; Graham 1992). Because slopes are steep, catenary sequences that dominate soils in other African savannas are not distinct in this area (Graham 1992).

Hluhluwe iMfolozi Park experiences summer rainfall, which falls predominantly between October and March. Rainfall is generally thought to be unimodal (Brooks & MacDonald 1983), although there is some evidence of bimodal summer rainfall (Ezemvelo KZN Wildlife 2002). Rainfall is closely linked to elevation within the park (Balfour & Howison 2001), producing a rainfall gradient between higher elevation Hluhluwe and lower elevation iMfolozi. Over the past five years, daily temperatures have ranged between ~39°C (mean daily T_{max}) and ~15°C (mean daily T_{min}) in summer and between ~32°C and ~9°C in winter in Hluhluwe, and between ~40°C and ~14°C in summer and between ~34°C and ~6°C in winter in iMfolozi (Zululand Tree Project data, unpublished). However, rainfall varies considerably from year to year. The longest running rainfall record in the park, from Hilltop Camp in Hluhluwe and spanning 1934 to present, shows a maximum annual rainfall of 1600mm in 1957/1958 and a minimum of 515mm in 1991/1992 (see Figure 2.2). This rainfall record suggests that rainfall cycles on an 18 year cycle of 9 wet years followed by 9 dry years (Ezemvelo KZN Wildlife 2002).

Vegetation is variable and heterogeneous throughout Hluhluwe iMfolozi Park. The high rainfall hills of Hluhluwe support forest patches where *Celtis africana* and *Harpephyllum caffrum* dominate (Whateley & Porter 1983). Mucina and Rutherford (2006) classify these Hluhluwe forests as Scarp forest (FOz5). However, the majority of Hluhluwe iMfolozi Park is savanna, classified as Northern Zululand Sourveld (SVI22) and Zululand Lowveld (SVI23) (see also Acocks 1975). *Spirostachys africana* forms extensive and often monospecific woodlands in riverine areas and drainage lines of Hluhluwe and iMfolozi. In addition, thicket precursor vegetation is becoming more widespread throughout the park, featuring *Euclea divinorum, E. crispa*, and *E. racemosa* in Hluhluwe and *E. divinorum* and *E. undulata* in iMfolozi as well as *Dichrostachys cinerea* and *Gymnosporia senegalensis* in both. However, half the park remains dominated by grasslands and open woodlands which prominently feature acacias, on which this thesis focuses (see Figure 2.3) (Whateley & Porter 1983). *Acacia karroo, A. nilotica, A. caffra, A. gerrardii*, and *A. burkei* are widespread in Hluhluwe; *A. nigrescens, A. tortilis*, and *A. grandicornuta* are restricted to and dominant in parts of iMfolozi, although other acacias also occur. Whateley and Porter (1983) give the most recent thorough overview of vegetation communities and their distribution throughout the Hluhluwe iMfolozi Park. Grass communities have been treated less thoroughly. Both bunchgrass areas, dominated by *Themeda triandra* and *Cymbopogon excavatus* (Whateley & Porter 1983), and grazing lawns, featuring *Urochloa mossambicensis* and *Digitaria longifolia* (Archibald *et al.* 2005), are common throughout the park.

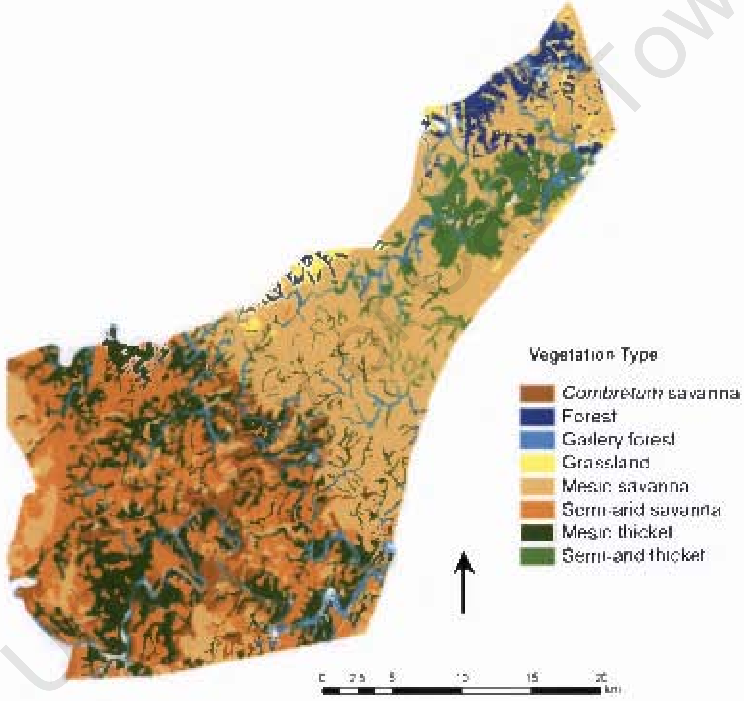

Figure 2.3. Broad vegetation types in Hluhluwe iMfolozi Park, derived from Whateley and Porter (1983).

The vegetation of Hluhluwe iMfolozi Park has undergone substantial changes through time. Bush encroachment has certainly been a problem over large areas, as documented by comparisons of vegetation classifications and maps from 1937 to 1975 (Henkel 1937; Watson & MacDonald 1982; Whateley & Porter 1983) and of aerial photography from the 1960s to present (Wigley 2007). Changes in the grass layer have also occurred. Watson and MacDonald (1982) suggest that 'overgrazed' short-grass areas expanded at the expense of bunchgrass areas from 1937 to 1975; overgrazing was certainly a major perceived concern during the 1960s and 1970s (Mentis 1968; Watson & MacDonald 1982). However, Bond *et al.* (2001) suggest that the proportion of grazing lawn in the park may have actually decreased, possibly in response to management practices aimed at homogenizing the impact of grazers on the landscape.

A SHORT HISTORY OF HLUHLUWE IMFOLOZI PARK

The area in and around Hluhluwe iMfolozi Park has a long history of human occupation, during which people may have played an important role in shaping its ecological landscape. The earliest remains of anatomically modern humans in KwaZulu Natal date from as early as 170,000 years ago from Border Cave on the Swaziland border (Miller *et al.* 1999; Grün & Beaumont 2001), approximately 80 km from Hluhluwe iMfolozi Park, although human ancestors had certainly been present in the area for millions of years before. Stone tools and human remains dating from 79 to 60 thousand years ago at Border Cave (Grün & Beaumont 2001) and from 61 to 26 thousand years ago at Sibudu Cave near Durban (Wadley & Jacobs 2004) indicate that the area was heavily utilized by nomadic hunter-gatherers. Extensive animal remains, including zebra, giraffe and impala, indicate that hunting was important (Plug 2004). Although Sibudu Cave is found in an area now dominated by forests (Wadley & Jacobs 2004), the animal species and plant remains found in the cave indicate that savannas may have been more widespread during the Stone Age than they are today (Plug 2004; Wadley 2004). These

Stone Age inhabitants also used fire, traces of which can be found in the cave as charcoal (Wadley 2004).

The first evidence of sedentary agriculture dates from approximately 200 to 300 AD, when the first Bantu-speaking peoples began immigrating to the area, probably from West Africa, marking the beginning of the Iron Age (Hall 1978; Hall 1987). These people cleared land for cereal farming, particularly sorghum, kept domesticated cattle, sheep, and goats, and smelted iron (van der Merwe 1980; Hall 1987; Maggs & Whitelaw 1991). In some parts of Africa, extraction of wood for iron smelting is thought to have had major effects on vegetation structure (Goucher 1981; Hall 1984; Feely 1985). Around 1000 AD, an abrupt break in the nature and content of archaeological sites signals the beginning of the Late Iron Age (Maggs & Whitelaw 1991). The Late Iron Age is characterized to some extent by cultural diversification and fragmentation throughout southern Africa and in Zululand in particular. People appear to have moved from valleys up to the hills, and settlements became smaller (Maggs 1980). This change in settlement patterns, as well as changes in types of settlements, indicates that production of cereals may have become less important and cattle more important agriculturally and culturally during this period (Maggs 1980; Hall 1987). Alternatively, people may have started to use wood, which does not preserve well, in the construction of large permanent settlements in valley bottoms, indicating that populations expanded into rather than moved into the hills (Maggs 1980). However, there is no doubt that when the second wave of Bantu-speaking immigrants arrived during 15th century from Zimbabwe (van der Merwe 1980), the Zululand area was already extensively populated and farmed.

Between 1818 and 1828, Shaka consolidated the fragmented and culturally diverse Zulu peoples into the Zulu Kingdom. He declared a royal hunting ground in the area at the confluence of the White and Black iMfolozi Rivers (see Figure 2.1), which is likely the first form of wildlife protection the area had experienced. Hunting may have contributed to suppressing and restricting wildlife populations during and before this period (Brooks & MacDonald 1983). Fire probably burned with annual to biennial frequency in this pre-colonial era (Emslie 1999), although variable rainfall probably contributed to variability in fire regimes even then.

With the subsequent expansion of European colonialism into the region, disease kept the Hluhluwe iMfolozi area sparsely populated throughout the 19th century (Lincoln 1995). Both *nagana* and malaria were prevalent in the area. *Nagana* in particular plays an important part in the history of the area. Caused by the *Trypanosoma* parasite and also known as trypanosomosis or livestock sleeping sickness, it essentially precluded cattle ranching in parts of Zululand through to Kruger National Park and other parts of Africa, where it was common. It is borne by tsetse flies (*Glossina* sp.), which breed at the boundary between savanna and bush. Tsetse feed primarily on the blood of wildlife, including zebra (*Equus burchelli*), wildebeest (*Connachaetes taurinus*), and buffalo (*Syncerus caffer*). For this reason, game was perceived to be responsible for the prevalence of *nagana*. In fact, a major rinderpest epidemic that lasted from 1895 to 1903 that decimated game populations resulted in major reductions in tsetse fly numbers and in the prevalence of *nagana*. Unlike in the Transvaal and Kruger NP area, however, where neither tsetse flies nor *nagana* ever recuperated after the rinderpest epidemic (Fuller 1923), tsetse recuperated in Zululand (Fuller 1923). *Nagana* prevalence had returned to pre-rinderpest levels by 1907, and game populations recovered relatively quickly (Henkel 1937).

For this reason, the early history of Hluhluwe and iMfolozi in particular is characterized by tension between highly political attempts to eradicate the disease by the large-scale slaughter of game and efforts to protect threatened wildlife species (Lincoln 1995), including the then critically endangered white, or square-lipped, rhinoceros (*Ceratotherium simum simum*). Hluhluwe and iMfolozi Game Reserves were declared independently in 1895 (see Figure 2.1); the corridor area was administered as Crown Land and effectively formed a part of the reserve complex, although it was only incorporated into the reserve in 1982. However, settlement of Northern Zululand intensified during the same period, and pressure to eradicate tsetse and *nagana* mounted (Lincoln 1995). Early efforts took the form of large-scale eradication of game, in direct conflict with stated conservation goals. Veterinary Services for the province instituted the first *nagana* campaign between 1916 and 1929, slaughtering thousands of heads of game (Lincoln 1995; Ezemvelo KZN Wildlife 2002). As research into tsetse fly developed, Veterinary Services switched to Harris traps to control fly populations in 1930, resulting in reduced pressure on ungulate populations. The traps were relatively ineffective, however. By 1939, pressure to eradicate tsetse and *nagana* had mounted again, and thousands more head of game were slaughtered (Ezemvelo KZN Wildlife 2002). Tsetse and *nagana* persisted, and in 1947 the second official *nagana* campaign began. The only unexplored option was spraying insecticides. Large areas of iMfolozi Reserve were sprayed with DDT between 1945 and 1947, with conclusive effects on tsetse fly populations, other insect life, and on the area's water supply (Lincoln 1995;

Ezemvelo KZN Wildlife 2002). In addition, bush clearing experiments began as an attempt to eliminate tsetse flies' breeding habitat, and culling of game continued. By 1952, when *nagana* was effectively eliminated, game stocks in Hluhluwe and iMfolozi had been decimated, and game had been eliminated from unprotected areas of the province. Giraffe and impala were eliminated from Hluhluwe by 1929 (Mentis 1968), and by 1952 no wildebeest or zebra remained in iMfolozi Game Reserve (Ezemvelo KZN Wildlife 2002). In Hluhluwe, where pressure to eradicate *nagana* was somewhat less intense, small populations of game survived, while in iMfolozi, animal populations were decimated (see Figure 2.4 & Figure 2.5). Animals were able to travel between the reserves via the Corridor, however, which was a key factor in the subsequent recuperation of game populations.

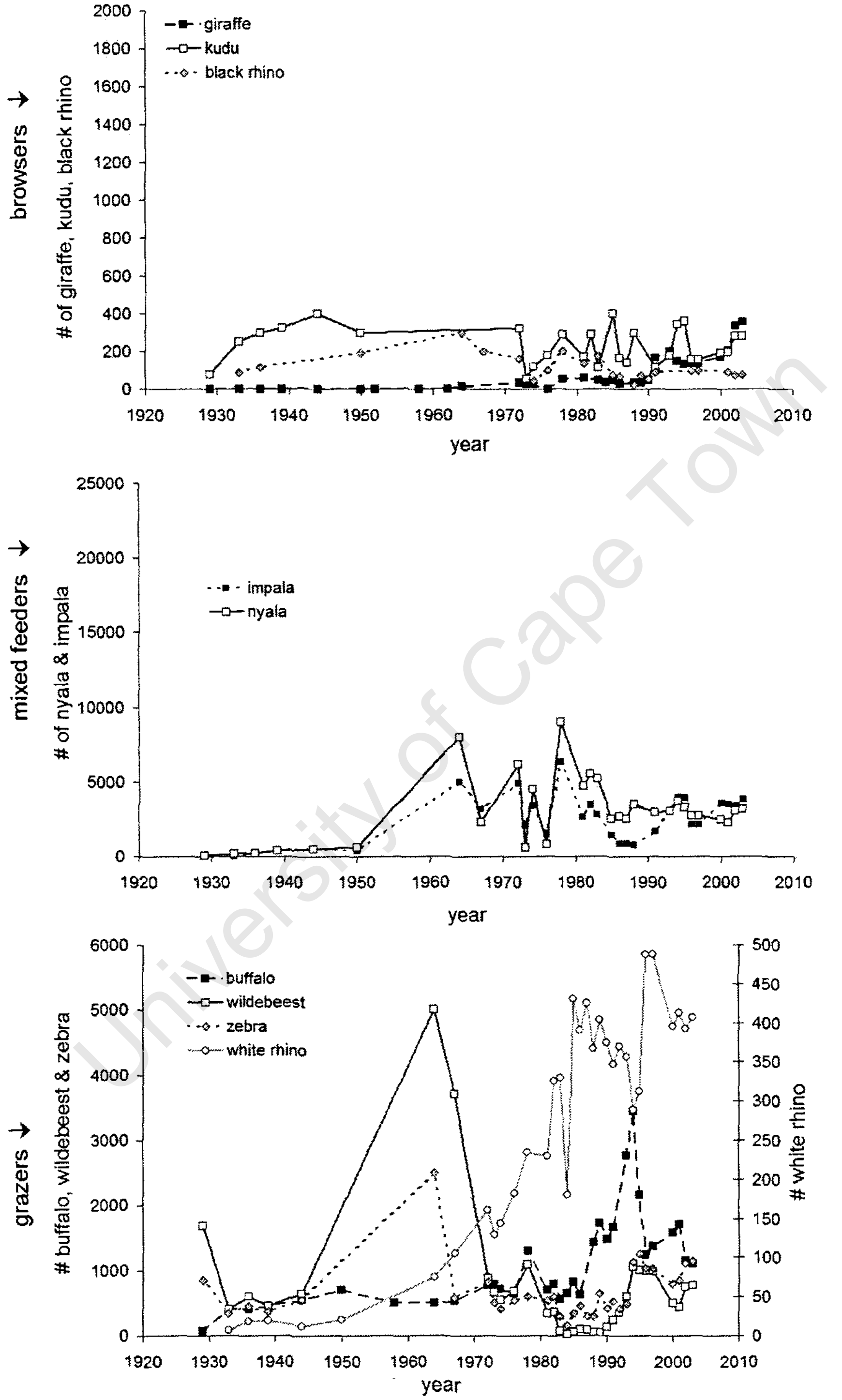

Figure 2.4. Numbers of dominant grazer, mixed feeder, and browser species in Hluhluwe Game Reserve. Compiled by Sue Janse van Rensburg from Hluhluwe iMfolozi Park management reports.

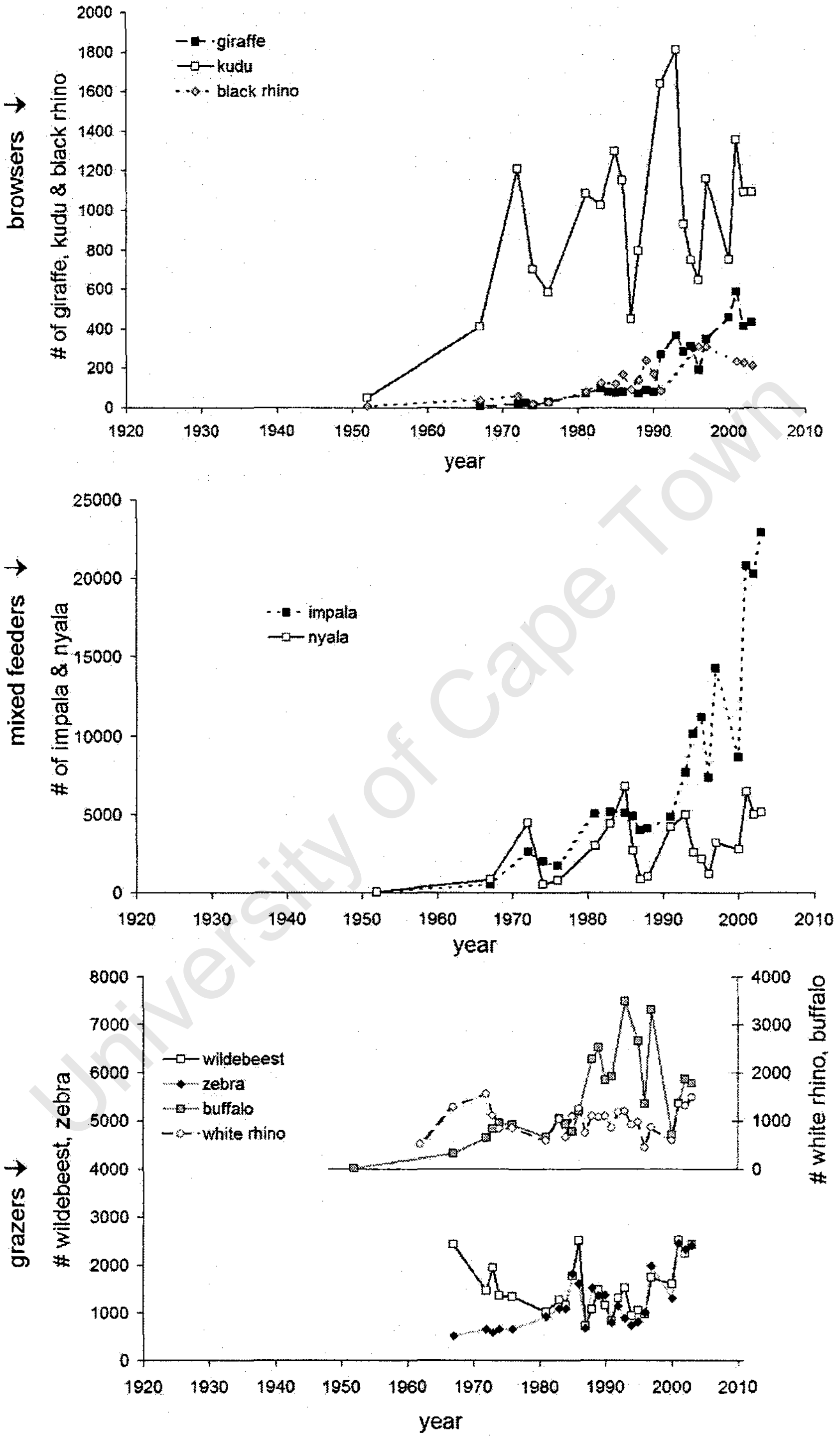

Figure 2.5. Numbers of dominant grazer, mixed feeder, and browser species in iMfolozi Game Reserve. Compiled by Sue Janse van Rensburg from Hluhluwe iMfolozi Park management reports.

Major changes in the animal ecology of the reserves also occurred over the same time period, even independent of the devastating anti-*nagana* campaigns. Both reserves essentially eradicated carnivores, shooting lions (*Panthera leo*) and poisoning hyenas (*Crocuta crocuta*); only substantial numbers of leopard (*Panthera pardus*) remained by 1930 (Brooks & MacDonald 1983). Lion were re-introduced in 1967, and elephant in 1978 (Ezemvelo KZN Wildlife 2002). Species assemblages of herbivores changed permanently, as specialist niche-feeders, including reedbuck (*Cerircapra arundinum*), mountain reedbuck (*Cerircapra fulvorufula*), klipspringer (*Oreotragus oreotragus*), steenbuck (*Raphiceros campestris*), and eland (*Taurotragus oryx*), went locally extinct (Henkel 1937). Following declaration of both reserves, animal movements became increasingly restricted both because of increasing human population densities outside the park and by the gradual fencing of the reserve. This probably had major impacts on animal movements and may have intensified animal impacts within the reserve by decreasing temporal variation in landscape use (Brooks & MacDonald 1983).

During the early history of the reserves until 1952, fire was rarely discussed and was not managed for explicit vegetation objectives; no vegetation management goals are documented from this period. In Hluhluwe, fire was used primarily in winter to ensure forage flow, to encourage herbivores to remain inside the reserve while it remained unfenced, and to aid game viewing for tourists (Brooks & MacDonald 1983). In iMfolozi, fire suppression was standard practice, and only occasionally did an accidental fire burn part of the reserve (Emslie 1999). The management of fire in savanna parks in general was not rationalized during this period, and both burning for forage flow and fire suppression was in line with fire management policy in larger parks such as Kruger NP (Biggs & Potgeiter 1999; van Wilgen *et al.* 2000).

The first research officer was appointed to the Hluhluwe iMfolozi area in 1952. Management policy was officially described as aiming "to maintain all species at present found within the reserve. This means trying to maintain a balance among the animals and between them and the soil, the vegetation and the water supplies. Ideally, this may be interpreted as maintaining the habitats as they occurred in the days prior to the restriction of game movements" (in Brooks & MacDonald 1983). The rationalization of ecological and 'scientific' conservation objectives represents a shift from 'single-species' conservation focusing on the white rhinoceros to conservation focusing on a multitude of species. Nonetheless, the system was viewed as a stable, equilibrium entity; preservation of extant systems remained the conservation goal, in line with the global conservations paradigm at the time (Pickett *et al.* 1992). Management actions changed little despite a shift in explicit conservation objectives.

An assessment of Hluhluwe in 1952 detected what was perceived as severe vegetation and soil degradation attributed to overburning and to extreme grazing and browsing pressure, exacerbated by the effects of a long drought (Brooks & MacDonald 1983). Game culling began in Hluhluwe in 1954 and intensified in 1959, focusing on 'gregarious grazers' thought to have major effects on vegetation cover. Nonetheless, densities of wildebeest and zebra recovered substantially after the end of the *nagana* campaigns (see Figure 2.4). Burning for forage flow continued, but management's emphasis changed to focus on preventing shrub encroachment into grasslands. From 1955, fire breaks were employed and controlled burns set following the first spring rains of the year. Bush clearing continued in some areas (Brooks & MacDonald 1983). A similar assessment in iMfolozi revealed 'good' veld conditions arising from low animal populations following the *nagana* campaigns. Culling continued, but focused on species perceived to be competitors with white rhino, which continued as the conservation focus of the reserve; wildebeest and zebra were completely excluded from iMfolozi and warthog (*Phacochoerus aethipicus*) were culled extensively (Brooks & MacDonald 1983). From the 1960s, herbivore population management changed to parallel rainfall; more animals were culled in dry years, when veld condition was worse, and fewer in wet years, when veld condition was better (see Figure 2.5). However, from 1974, herbivore management changed to emphasize managing the spatial use of the landscape by herbivores. This was done primarily by using fire to attract herbivores to underutilized areas and to rest short-grass grazing lawns, which were perceived to be 'degraded'. Autumn and spring burns were recommended for this purpose (Brooks & MacDonald 1983).

iMfolozi's fire policy was rationalized, but fire frequencies remained low. Most areas in the Hluhluwe Reserve, including areas of relatively low rainfall, have burned more than 10 times between 1956 and 1996, while most areas in the iMfolozi Reserve have burned only between one and eight times during the same period (Balfour & Howison 2001). Overgrazing became an increasing concern even in iMfolozi as herbivore populations increased (Mentis 1968). In both reserves, managers remained concerned with degraded veld condition and with managing herbivore impacts to allow areas of savanna to recuperate (see Figure 2.5).

Hluhluwe iMfolozi Park has undergone an explicit change in management policy in the last decade to "process-based" management of herbivory and fire (Ezemvelo KZN Wildlife 2002) in line with a change in the global conservation paradigm (Pickett *et al.* 1992). The park's management plan acknowledges that the park is a product of a human and ecological history and that ecological processes, including herbivory and fire, clearly do not function as they did in the pre-colonial landscape. For this reason, management aims to replicate these processes as they might have functioned in an intact landscape. This management plan poses a new set of challenges and questions. We have no clear understanding of how climate, fire and herbivore populations over the past century have shaped the savannas that we see in Hluhluwe iMfolozi Park today, and of how they should be managed in future for an explicit set of conservation and management goals.

Chapter 3

Fire, herbivory, and the grass layer contribute to structuring *Acacia* communities in an African savanna

A. Carla Staver & William J. Bond

Introduction

Savannas are defined as having a continuous grass layer with a discontinuous tree layer, and the 'savanna problem' – explaining tree-grass coexistence – dominates savanna ecology (Sarmiento 1984; Skarpe 1992; Scholes & Archer 1997; Sankaran *et al.* 2005). Most authors agree that a combination of climatic and edaphic variables in combination with fire and herbivory contribute to tree-grass coexistence, though some emphasize an equilibrium-based 'bottom-up' control (Walter 1971; Walker & Noy-Meir 1982) while others emphasize variability and disturbance. Tree-grass ratios fluctuate widely over short and long time periods (Walker *et al.* 1981; Westoby *et al.* 1989; Gillson 2004) and they are often not at equilibrium with climate (Bond 2005; Bond *et al.* 2005; Sankaran *et al.* 2005). Both fire (Eckhardt *et al.* 2000; Moreira 2000; van Wilgen *et al.* 2003; D'Odorico *et al.* 2006) and herbivory (du Toit 2003; Sharam *et al.* 2006) may account for much of the variability and heterogeneity in savanna systems.

Fire has been shown to suppress tree cover below its theoretical 'climate maximum' in savannas worldwide (Bond 2005; Bond *et al.* 2005; Sankaran *et al.* 2005), and herbivory by native herbivores can prevent tree recruitment in systems with extant native herbivore assemblages (Prins & van der Jeugd 1993; Barnes 2001; Augustine & McNaughton 2004). Nonetheless, trees do establish despite fire and herbivory. Saplings persist under conditions of frequent fire or intense browsing until they are able to escape or are released and recruit into adults (Prins & van der Jeugd 1993; Higgins *et al.* 2000). Some savanna saplings have adapted a unique set of characteristics for surviving environments with frequent fire, including the ability to resprout from stored root starch reserves (Hoffmann *et al.* 2003; Hoffmann *et al.* 2004) and growth form and architecture specializations (Gignoux *et al.* 1997; Archibald & Bond 2003; Hoffmann & Solbrig 2003). Other savanna saplings have adapted characteristics for dealing with herbivory, including chemical, structural and architectural defenses against herbivory (Grubb 1992; Gowda 1996; Marquis 1996; Gowda 1997; Stowe *et al.* 2000; Archibald & Bond 2003; Rooke *et al.* 2004). Species have clearly evolved a variety of strategies for coping with frequent and intense disturbances from fires and from herbivory.

However, the potential for the same determinants of savanna structure to impact on composition of vegetation communities in savannas is largely unknown. Community ecology has traditionally focused on competition as the mechanism for structuring community assembly and for shaping species' responses to their environments (Connell 1961; MacArthur 1970; May & MacArthur 1972; Keddy & Shipley 1989; Chesson 2000; Tilman 2004). The role of competition in structuring communities is not universal; major disturbances are often considered to prevent systems from reaching competitive equilibrium (Huston 1979; Pickett & White 1985). However, despite the acknowledged role of disturbance in shaping community dynamics, community ecology and savanna ecology in particular often focus instead on the role of physiological growth constraints in restricting species distributions (Williams *et al.* 1996; Scholes *et al.* 2002; Silvertown 2004). If fire and herbivory are important in limiting tree recruitment, they could also be important in structuring woody plant assemblages. Well-defended saplings would survive best in heavily browsed areas, whereas saplings tolerant of fire would dominate in frequently burnt areas. Species assemblages would be structured by type and intensity of disturbance experienced by juveniles. However, there are few examples of community assembly structured by differential species' responses to disturbance (Grimm 1984; Bond *et al.* 2001), despite the potential for fire and herbivory to have major effects in structuring communities in savanna ecosystems.

Competition of trees with grasses for water has long been a major concern of savanna ecology. If trees and grasses compete for water, how are they able to coexist? The 'Walter hypothesis' suggests that if competition among trees and among grasses is stronger then competition between trees and grasses via a separation in rooting depth, stable coexistence should be possible (Walter 1971; Walker & Noy-Meir 1982; Higgins *et al.* 2000). In fact, tree-grass coexistence is not stable (Walker *et al.* 1981; Westoby *et al.* 1989; Gillson 2004), trees often do compete with grasses directly for water (Koukoura & Menke 1995; Le Roux *et al.* 1995; Mordelet *et al.* 1997; Weltzin & McPherson 1997), and competition for water, nutrients and even light between grasses and trees, especially tree seedlings, may affect tree demographics in savannas (Menaut *et al.* 1990; Davis *et al.* 1999). If species respond differently to competition with grasses, variation in the grass layer could also structure woody plant assemblages. Nonetheless, studies of responses of seedling and sapling distributions to a dynamic grass layer in savanna landscapes are rare (but see Archer 1990; Brown & Archer 1999).

This paper reports the results of a study investigating distributions of common *Acacia* species along fire frequency, herbivore use intensity and grass biomass and cover gradients in Hluhluwe iMfolozi Park in KwaZulu Natal, South Africa. We were interested in determining the degree to which species' ability to deal with disturbances determines their distribution and the extent to which that disturbance determines community assembly. *Acacia* species are dominant throughout the park; the most common species, which were included in this analysis, include *A. caffra*, *A. gerrardii*, *A.*

karroo, *A. nilotica*, *A. grandicornuta*, *A. nigrescens*, and *A. tortilis*. *Acacia* species occurrence, herbivore use, fire history, and grass biomass and cover were recorded for plots distributed throughout the park, sampled in June to August of 2007. We analyzed whether these gradients explained variation in probability of occurrence of each species and whether they improved predictions of species co-occurrence relative to a null model.

Acacia architecture may be expected to differ in frequently burnt areas and in areas with intense herbivory. Archibald and Bond (2003) found intraspecific variation in *A. karroo* sapling architecture, with pole-like forms occurring in frequently burnt areas and densely ramified cage-like forms where browsing was intense. We characterized sapling architecture to determine whether the distribution of species along gradients was correlated with differences in architectural traits related to herbivory and fire.

Study Area

The study was conducted in Hluhluwe iMfolozi Park (900 km^2; 28°00' – 28°26' S; 31°43' – 32°09' E), located in northern KwaZulu Natal, South Africa. Topography is varied, consisting mainly of rolling hills of up to 540m elevation in the Hluhluwe Game Reserve area falling into broader river valleys at 40m elevation in the iMfolozi Game Reserve area. Soil types are closely linked to bedrock geology (Graham 1992), consisting predominantly of shales and sandstones with intermittent doleritic intrusions (King 1970; Graham 1992). Because slopes are steep, catenary sequences that dominate soils in other African savannas are not distinct in this area.

Rainfall is closely linked to elevation within the park (Balfour & Howison 2001), producing a rainfall gradient between higher elevation Hluhluwe GR and lower elevation iMfolozi GR. The longest rainfall series comes from Hilltop Tourist Camp in Hluhluwe, where rainfall in the park is highest, and spans 1933 to 2006. Average annual rainfall was 974mm. A maximum rainfall of 1594mm fell during the 1957/1958 season and a minimum of 517mm during the 1991/1992 season. Hluhluwe daily temperatures range between ~39°C (mean daily T_{max}) and ~15°C (mean daily T_{min}) in summer and between ~32°C and ~9°C in winter. iMfolozi daily temperatures range between ~40°C and ~14°C in summer and between ~34°C and ~6°C in winter (Zululand Tree Project baseline data).

Fire frequency in the park varies with rainfall; areas of high fire frequency have burned more than 10 times between 1956 and 1996, while areas of low fire frequency burned as little as once during the same period (Balfour & Howison 2001). Large mammal herbivore densities within and between reserves vary depending on herbivore habitat preferences. Impala (*Aepyceros melampus*) are by far the most numerous herbivore in the park and occur with higher densities in semi-arid iMfolozi (36 per km^2) than in mesic Hluhluwe (24 per km^2); white rhino (*Ceratotherium simum*) make up the largest biomass in the park with higher densities in iMfolozi (2.5 per km^2) than Hluhluwe (1.8 per km^2). Herbivore densities have fluctuated substantially during the past century in Hluhluwe iMfolozi Park, largely due to hunting, the rinderpest epidemic, and culling campaigns during the early part of the 20th century associated with efforts to eradicate the *nagana* livestock disease. However, herbivore densities have recuperated, and the park currently employs drought mitigation strategies, including limiting fire during dry periods and controlling animal populations, to minimize widespread death of game from drought.

Methods

COMMUNITY COMPOSITION

Acacia savanna communities were sampled next to roads throughout Hluhluwe iMfolozi Park during June through August of 2007. Transects of 40m x 10m ran perpendicular to the road starting 30m from the side of the road. Species and height were recorded for all trees in the transect, and diameter at breast height (1.4m) was recorded for tree stems with circumference greater than 10cm. Measuring height of tree allowed us to differentiate between saplings (height $\leq$ 2m) and adults (height $\geq$ 3.5m) and evaluate whether they respond to gradients differently. Grass biomass was measured with a disc pasture meter (DPM) every two meters along the transect (see Bransby & Tainton 1977). DPM reading were converted to grass biomass using the following equation:

$$\text{grass biomass in g m}^{-2} = 12.6 + 26.1 * \text{DPM}$$

calibrated for 1735 samples (R^2=0.73). At each DPM reading, percent cover was estimated and grass species recorded. All dung in the transect was identified and counted as numbers of piles.

We placed transects at 500m intervals along roads. A total of 202 sites were distributed throughout the park (see Figure 3.1), except in the iMfolozi Wilderness Area, where there is no road access. We did not sample in dense thicket, where *Acacia* saplings are rare, or *Spirostachys africana* woodlands, which occur predominantly in drainage lines and where *Acacia* saplings and adults except of *A. robusta*, a riverine species, are rare. We sampled primarily along open-access dirt roads and avoided large paved roads because of concerns about edge effects.

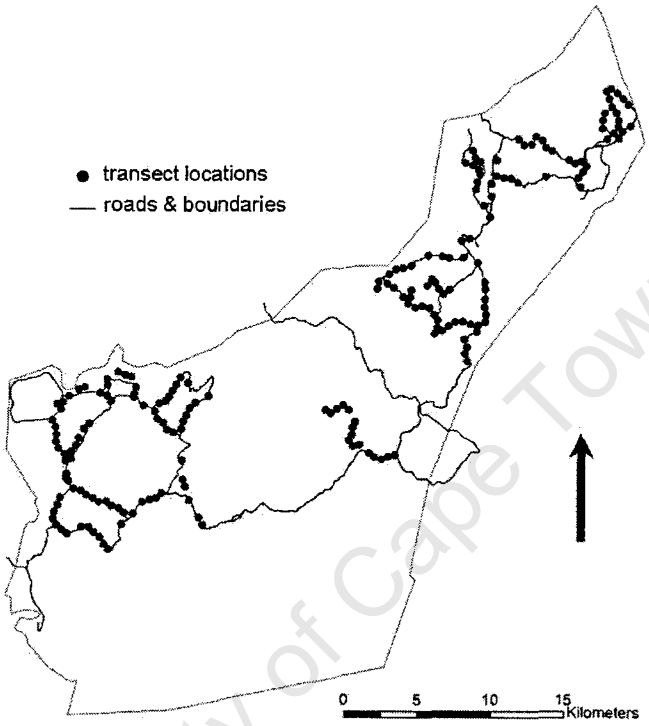

Figure 3.1. Map of Hluhluwe iMfolozi Park with road network and distribution of plots.

Dung counts were used as surrogates for herbivore use. Although herbivore population estimates are available for the park, there are no spatially explicit estimates suitable for examining herbivore impacts on a community scale. However, spatially explicit fire records are available; frequency of fires over the past 20 years at each site was extracted from Hluhluwe iMfolozi Park records. Although rainfall varies substantially throughout the park, spatially explicit rainfall records are not available. However, rainfall increases as elevation increases (Balfour & Howison 2001) and we have used elevation as a surrogate for rainfall.

SPINESCENCE AND ARCHITECTURE

Sapling architecture was measured for 25 saplings of each species (except *A. caffra*). For each individual, we measured vertical height of the sapling and the number, length, and position of all primary branches emerging from the main stem. On every third primary branch, we recorded the total number of secondary branches emerging from the branch and then measured thorn length, width, and leaf length for the middle three thorns on the branch. From this information, we have calculated overall primary branch density per meter of sapling height, secondary branch density per meter of primary branch, average spine length and width, and average length of the longest leaf at each spine. This is a simple yet effective way to characterize the branching and spinescence of *Acacia* saplings.

ANALYSIS

Species Occurrence along Gradients

Distribution and co-occurrence of *Acacia* saplings (height ≤ 2m) and adults (ht > 3.5m) were analyzed relative to gradients in elevation, grass biomass and cover, dung counts, and local fire frequency. Each common *Acacia* species was classified as present or absent in each plot. Gradients were divided into classes with at least 7 plots in each class. Classes were equal sized except where classes had fewer than 7 plots, when adjacent classes were combined until all classes along a gradient had at least 7 plots. For instance, plots that burned once or twice were combined and plots that burned either 13 or 14 times were combined, but integer classes were used for all other fire frequencies (see Figure 3.2 for an example). Probability of occurrence of each species was calculated for each class along each gradient (for an illustration of raw data and of corresponding probability of presence along a fire gradients, see Figure 3.2). Relationships between the gradient and probability of presence were usually linear or quadratic; lines of fit and regressions were calculated using one- or two-term best subset polynomial regression in STATISTICA V6 (StatSoft 2004). In cases were linearity was not rejected, we used standard linear regression.

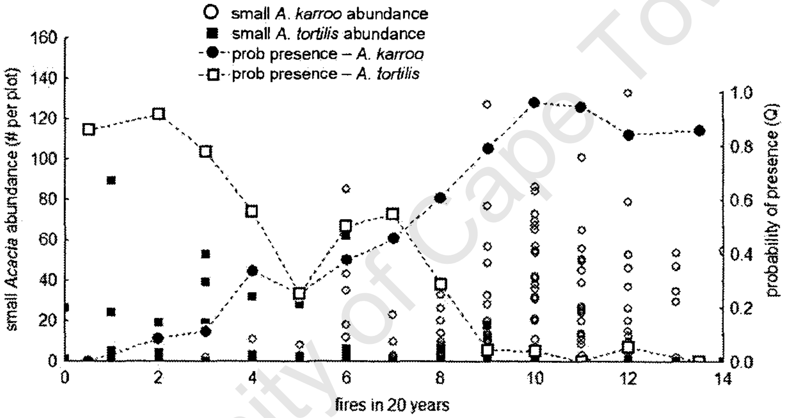

Figure 3.2. Sapling abundance and probability of sapling presence vs. fire frequency for *A. karroo* and *A. tortilis*. Probability of sapling presence was calculated for each class along gradients. Gradients were divided into classes with at least 7 plots. Classes were equal sized except where classes had fewer than 7 plots, when adjacent classes were combined, e.g. plots burned 1 to 2 times were combined and plots that burned 13 to 14 times were combined, but integer classes were used for all other fire frequencies.

Species Co-occurrence along Gradients

To determine whether these gradients were important in structuring community composition and species co-occurrence, we compared observed co-occurrence for each species pair (total number of plots with both species present) with expected co-occurrence of each species pair. Observed and expected co-occurrence were compared using a χ^2-test with four categories: 1) both species present, 2) only species A present, 3) only species B present, and 4) neither species present, resulting in three degrees of freedom. We first tested whether species co-occurrence was totally random by comparing observed co-occurrence (observed $N_{both} = N_{tot}*p[A+B]$) to expected co-occurrence assuming that co-occurrence is totally random on the landscape for each species pair:

$$\text{expected } N_{both} = N_{tot}*p[A]*p[B]$$

$$\text{expected } N_{only\ A} = N_{tot}*(p[A] - p[A]*p[B])$$

$$\text{expected } N_{only\ B} = N_{tot}*(p[B] - p[A]*p[B])$$

$$\text{expected } N_{neither} = N_{tot} - N_A - N_B - N_{A+B}$$

In this case, the null model was random co-occurrence; we evaluated whether species co-occurrence patterns would be adequately explained by random occurrence in the landscape or whether additional structure was needed to explain co-occurrence patterns.

We evaluated whether using species responses to gradients to predict rates of co-occurrence improved predictions of rates of co-occurrence. We calculated co-occurrence within each class along each gradient and summed all classes along a gradient, resulting in predictions of total co-occurrence in the landscape. We then compared observed co-occurrence to expected co-occurrence, assuming that co-occurrence was structured among *n* classes along each gradient but was random within each class:

$$\text{expected } N_{both} = \sum_{i=1}^{n} N_i*p_i[A]*p_i[B]$$

$$\text{expected } N_{only\ A} = \sum_{i=1}^{n} N_i*(p_i[A] - p_i[A]*p_i[B])$$

$$\text{expected } N_{only\ B} = \sum_{i=1}^{n} N_i*(p_i[B] - p_i[A]*p_i[B])$$

$$\text{expected } N_{neither} = N_{tot} - N_A - N_B - N_{A+B}$$

where N_i is the number of plots in category i, $p_i[A]$ is the probability of one species occurring in that category, and $p_i[B]$ is the probability of the other species occurring in that category. Fits of probability of occurrence with gradient were used to estimate probabilities of species presence in classes along each gradient. The Dunn-Sidak modification of the Bonferroni correction was used to modify thresholds for significance testing (Quinn & Keough 2002):

$$\alpha = 1 - (1 - 0.05)^{1/c}$$

where c is the number of comparisons; a total of 21 species-pairs were compared, resulting in α equal to 0.0024.

Improvement in accuracy of expected co-occurrence calculated along a gradient was interpreted as evidence that communities were structured along that gradient. Differences between expected and observed co-occurrence that persisted even when we used gradients were interpreted as evidence that some other factor was important in structuring communities in these savannas.

The role of gradients in regulating species distributions and coexistence were also analyzed via NMDS ordination in PC-Ord (McCune & Mefford 1999). Distances were calculated using Bray-Curtis dissimilarity. NMDS ordination was done with a maximum of 400 iterations, an instability criterion of 0.00001, starting with 6 axes, and 40 real and 50 randomized runs. Relationships of species compositions to disturbance gradients were calculated from Pearson's correlation analyses in NMDS joint plots.

Sapling Architecture and Relationship to Gradients

Species' sapling architecture was characterized by calculating primary and secondary branch density, average spine length, average spine width, and average leaf length for each individual. Differences among species were evaluated using non-parametric Kruskal-Wallis ANOVAs in Statistica (StatSoft 2004). We then calculated the mean and standard error of each architecture parameter as well as the mean and standard deviation of fire frequency and dung count of all plots in which each species was present. We evaluated whether architecture varied along these gradients using simple linear regression in Statistica (StatSoft 2004).

Figure 3.3. Photos of plots 26, 34, 107 and 203. Plot 26 was a bunchgrass area with mostly *A. karroo* saplings (93% grass cover, 700 g grass per m^2, and no dung). Plot 34 was also a bunchgrass area with mostly *A. karroo* saplings, but grass cover and biomass were less and herbivore pressure was more (64% grass cover, 235 g grass per m^2, and 6 dung piles). Plot 107 was a grazing lawn with *A. grandicornuta* (33% grass cover, 60 g grass per m^2, and 32 dung piles). Plot 203 was a grazing lawn with *A. gerrardii* saplings (53% grass cover, 80 g grass per m^2, and 42 dung piles). Differences in architecture are clear between fire-adapted species like spindly *A. karroo* and herbivore-adapted species like cagey *A. grandicornuta*.

Results

A total of 202 plots were sampled throughout Hluhluwe iMfolozi Park. Plots were ecologically diverse, ranging from grazing lawns, with low standing grass biomass, low fire frequency and high herbivore use, to bunchgrass savannas, with high standing grass biomass, high fire frequency and low herbivore use (see Figure 3.3). Grass biomass ranged from 31 g m^{-2} to 743 g m^{-2}. Grass cover ranged from zero percent to 100 percent. Dung counts numbered between zero and 212 piles per plot. Plots burned between zero and 14 times in the past 20 years. As expected, grass, herbivore use, and fire covaried (see Figure 3.4). Grass biomass (log transformed) and grass cover estimates

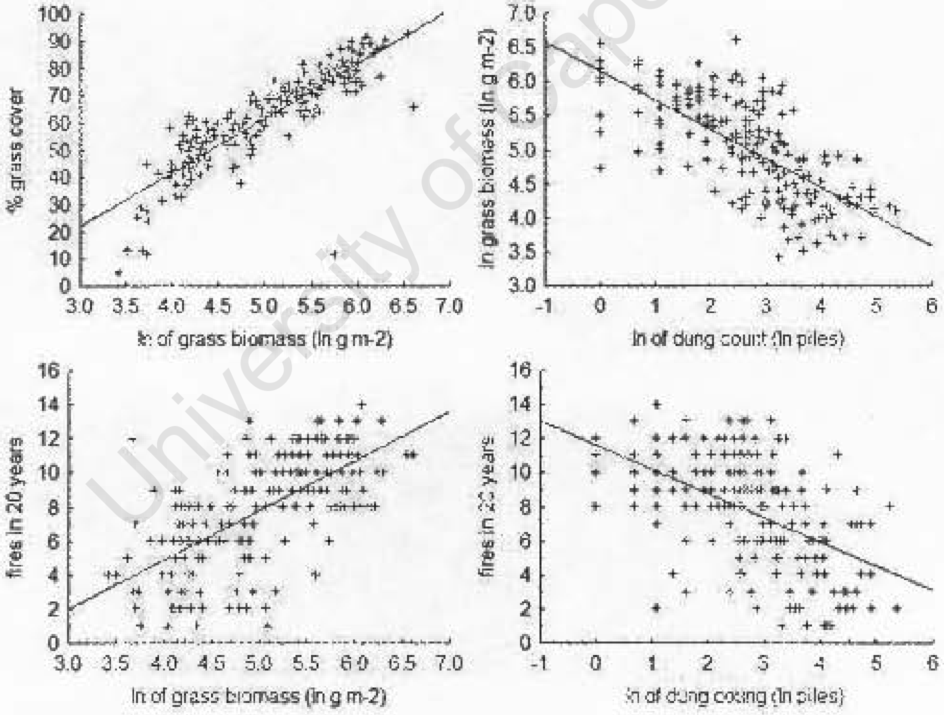

Figure 3.4. Covariation in grass biomass and cover, herbivore use, and fire gradients. Grass cover and grass biomass (R^2=0.741, p<0.0001), grass biomass and herbivore use (R^2=0.506, p<0.0001), fire frequency and grass biomass (R^2=0.424, p<0.0001), and fire frequency and herbivore use (R^2=0.281, p<0.0001) were all closely related. Fire frequency was related to grass biomass and herbivore use despite the fact that fire frequency was aggregated over the past 20 years and grass biomass and herbivore use estimates represent only the year data was collected: this relationship probably reflects some continuity and stability in communities in the landscape.

were closely related (R^2=0.741, p<0.0001). Grass biomass decreased with increasing dung counts (log transformed) (R^2=0.506, p<0.0001), whereas number of fires in 20 years increased with increasing grass biomass (R^2=0.424, p<0.0001). Similarly, grass cover also decreased with increasing dung counts (log transformed) (R^2=0.350, p<0.0001), and fire frequency increased with increasing grass cover (R^2=0.313, p<0.0001). Fire frequency decreased with increasing herbivore use (R^2=0.281, p<0.0001).

OCCURRENCE OF *ACACIA* ALONG GRADIENTS

Variation in species responses to these gradients was substantial, and the strength of these gradients in explaining trends in occurrence of *Acacia* species also varied. Abundances of saplings of different species varied substantially along gradients (see Figure 3.2). However, abundance is less central than probability of presence (Q) for characterizing where species occur along the gradient. Most of the analyses that follow use probability of presence of a species along sections of the various gradients.

Saplings

Elevation, as a surrogate for rainfall, was not a universal predictor of probability of presence of *Acacia* saplings (see Figure 3.5 and Table 3.1). Probability of presence of *A. caffra* and *A. karroo* saplings increased with increasing elevation/rainfall, although probability of finding *A. karroo* saplings was higher than 40% even at low rainfall. Probability of presence of *A. grandicornuta* and *A. nigrescens* saplings decreased as rainfall increased. *A. tortilis*, *A. nilotica*, and *A. gerrardii* sapling occurrence was not related to elevation/rainfall.

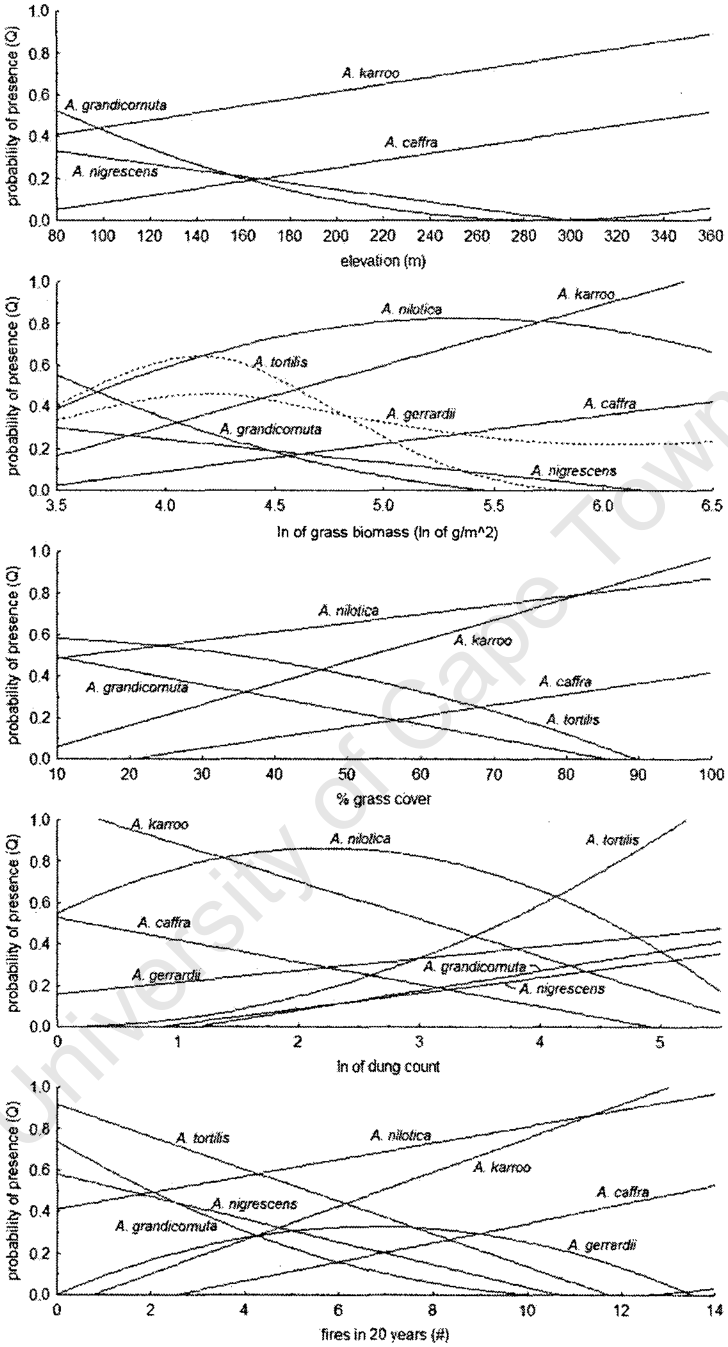

Figure 3.5. Probability of *Acacia* sapling occurrence along elevation, grass biomass and cover, dung count, and fire frequency gradients. Solid lines show linear or quadratic fits (see Table 1); dotted lines show least squared distance fits for species that had clear trends in probability of occurrence along the gradient but were not described by linear or quadratic relationships. *A. karroo* and *A. caffra* saplings occurred in areas with high grass biomass and cover, low dung counts, and high fire frequency. *A. nilotica* and *A. gerrardii* occurred at intermediate grass biomass and fire frequency. *A. grandicornuta, A. nigrescens* and *A. tortilis* occurred in areas with low grass biomass and cover, high dung counts, and low fire frequency.

Table 3.1. Probability of presence of *Acacia* saplings (ht ≤ 2m) along elevation, grass biomass and cover, herbivore use and fire frequency gradients. Polynomial regressions were done to define relationships between probability of occurrence (Q) of small *Acacia* trees and gradients, except where linearity was not rejected.

Probability of small *Acacia* presence		R^2	*p*	fit equation
elevation	*A. caffra*	0.484	0.017	$Q = -0.082 + 0.0017*elev$
	A. gerrardii		n.s.	
	A. karroo	0.618	0.0041	$Q = 0.027 + 0.0017*elev$
	A. nilotica		n.s.	
	A. grandicornuta	0.803	0.0006	$Q = 1.00 - 0.0069*elev + 0.000012*elev^2$
	A. nigrescens	0.809	0.0002	$Q = 0.45 - 0.0015*elev$
	A. tortilis		n.s.	
grass biomass (g/m^2)	*A. caffra*	0.686	0.042	$Q = -0.45 + 0.13*\ln(bm)$
	A. gerrardii		n.s.†	
	A. karroo	0.936	0.0016	$Q = -0.85 + 0.29*\ln(bm)$
	A. nilotica	0.865	0.023	$Q = -2.78 + 1.35*\ln(bm) - 0.13*\ln(bm)^2$
	A. grandicornuta	0.955	0.0043	$Q = 3.31 - 1.11*\ln(bm) + 0.093*\ln(bm)^2$
	A. nigrescens	0.837	0.011	$Q = -0.69 + 0.11*\ln(bm)$
	A. tortilis		n.s.†	
% grass cover	*A. caffra*	0.687	0.021	$Q = 0.11 - 0.0053*cover$
	A. gerrardii		n.s.	
	A. karroo	0.773	0.0091	$Q = -0.039 + 0.010*cover$
	A. nilotica	0.634	0.032	$Q = 0.44 + 0.0043*cover$
	A. grandicornuta	0.636	0.032	$Q = 0.56 - 0.0065*cover$
	A. nigrescens		n.s.	
	A. tortilis	0.559	0.032	$Q = 0.59 - 0.000073*cover^2$
dung count (piles)	*A. caffra*	0.575	0.018	$Q = 0.53 - 0.11*\ln(dng)$
	A. gerrardii	0.586	0.016	$Q = 0.16 + 0.057*\ln(dng)$
	A. karroo	0.842	0.0005	$Q = 1.06 - 0.18*\ln(dng)$
	A. nilotica	0.611	0.025	$Q = 0.55 + 0.29*\ln(dng) - 0.064*\ln(dng)^2$
	A. grandicornuta	0.745	0.0027	$Q = -0.11 + 0.096*\ln(dng)$
	A. nigrescens	0.765	0.0020	$Q = -0.066 + 0.076*\ln(dng)$
	A. tortilis	0.952	<0.0001	$Q = 0.036*\ln(dng)^2$
# of fires in 20 years	*A. caffra*	0.789	<0.0001	$Q = -0.12 + 0.046*fire$
	A. gerrardii	0.663	0.0017	$Q = 0.097*fire - 0.0072*fire^2$
	A. karroo	0.907	<0.0001	$Q = -0.064 + 0.082*fire$
	A. nilotica	0.420	0.017	$Q = 0.41 + 0.040*fire$
	A. grandicornuta	0.737	0.0006	$Q = 0.74 - 0.13*fire + 0.0058*fire^2$
	A. nigrescens	0.723	0.0002	$Q = 0.58 - 0.054*fire$
	A. tortilis	0.848	<0.0001	$Q = 0.92 - 0.078*fire$

† Probability of presence shows a clear pattern in relation to the driver. This relationship is not described adequately by either linear or polynomial regression.

Some *Acacia* species showed predictable trends in probability of sapling occurrence along a grass biomass gradient (see Figure 3.5 and Table 3.1). Probability of presence of *A. caffra* and *A. karroo* saplings increased with increasing grass biomass. Probability of presence of *A. grandicornuta* and *A. nigrescens* saplings decreased as grass biomass increased. *A. nilotica* saplings occurred most frequently at intermediate grass biomass. Probability of presence of *A. gerrardii* and *A. tortilis* saplings also showed clear patterns along a grass biomass gradient, but neither polynomial nor linear fits adequately described this relationship; probability of sapling presence increased to a peak at a relatively low grass biomass and decreased again. Although their probability of presence peaked at similar grass biomass, *A. gerrardii* sapling occurrence was less structured than *A. tortilis* sapling occurrence along the grass biomass gradient; *A. gerrardii* saplings occurred even at high grass biomass, while probability of presence of *A. tortilis* saplings declined to zero.

Some *Acacia* species also showed predictable trends in probability of sapling occurrence along a grass cover gradient (see Figure 3.5 and Table 3.1). Probability of presence of *A. caffra* and *A. karroo* saplings increased with increasing grass cover. Probability of presence of *A. nilotica* saplings also increased with increasing grass cover, but probability of presence was almost 50% throughout the entire range of grass cover. Probability of presence of *A. grandicornuta* and *A. tortilis* saplings decreased as grass cover increased. Grass cover was not significantly related to probability of presence of *A. gerrardii* or *A. nigrescens* saplings.

Dung counts and fire frequency were both more consistent predictors of probability of presence of *Acacia* saplings than elevation, grass biomass or grass cover (see Figure

3.5 and Table 3.1). Probability of presence of *A. caffra* and *A. karroo* saplings decreased with increasing herbivore use. Probability of presence of *A. grandicornuta*, *A. nigrescens* and *A. tortilis* saplings increased as herbivore use increased. Probability of presence of *A. gerrardii* saplings increased with increasing dung counts but was relatively high throughout the range of dung counts. *A. nilotica* saplings occurred most frequently at intermediate herbivore use.

Probability of presence of *A. caffra* and *A. karroo* saplings increased with increasing fire frequency. Probability of presence of *A. grandicornuta*, *A. nigrescens*, and *A. tortilis* saplings decreased as fire frequency increased, although *A. tortilis* and *A. nigrescens* saplings were tolerant of slightly higher fire frequency than *A. grandicornuta*. *A. gerrardii* and *A. nilotica* saplings occurred most frequently at intermediate fire frequency, but *A. nilotica* saplings peaked at a higher fire frequency than *A. gerrardii*.

Saplings of most species occurred even in plots where adults of the same species did not occur (see Table 3.2). More that 90% of the plots containing saplings of *A. caffra*, *A. gerrardii*, or *A. karroo* did not have conspecific adults in them, while 70% or more of the plots containing saplings of *A. nilotica*, *A. grandicornuta*, or *A. tortilis* did not have conspecific adults. Only *A. nigrescens* saplings appeared to be constrained to plots where adults of that species were also present, but adults are so widespread that this is not surprising. These results indicate that dispersal was probably not a limiting factor constraining distributions of *Acacia* saplings.

Table 3.2. Distribution of saplings relative to distribution of adults. Number and percentage of plots with saplings that have no adults, and number and percentage of plots with saplings that have no adults.

	N plots with saplings & adults	N plots with saplings & no adults	% of plots w/ saplings that also have adults	% of plots w/ saplings that have no adults
A. caffra	1	48	2 %	98 %
A. gerrardii	4	64	6 %	94 %
A. karroo	12	109	10 %	90 %
A. nilotica	45	103	30 %	70 %
A. grandicornuta	8	19	30 %	70 %
A. nigrescens	12	15	44 %	56 %
A. tortilis	8	52	13 %	87 %

Adults

Of 202 plots only one plot had large *A. caffra* trees and only four had large *A. gerrardii* trees; probability of presence of these species was not analyzed along gradients. In general, probability of large *Acacia* tree presence was less predictably related to gradients than *Acacia* sapling presence (see Figure 3.6 and Table 3.3). However, where adult presence was related to gradients, patterns were similar to sapling distribution patterns.

Probability of presence of *A. nilotica* adults peaked at intermediate elevation, grass cover, and grass biomass. Probability of presence of *A. grandicornuta* and *A. nigrescens* adults decreased with increasing elevation/rainfall and increasing grass biomass; probability of *A. nigrescens* adults also decreased with increasing grass cover. Probability of presence of *A. karroo* adults decreased with increasing herbivore use, while probability of presence of *A. grandicornuta* and *A. nigrescens* adults increased with increasing herbivore use.

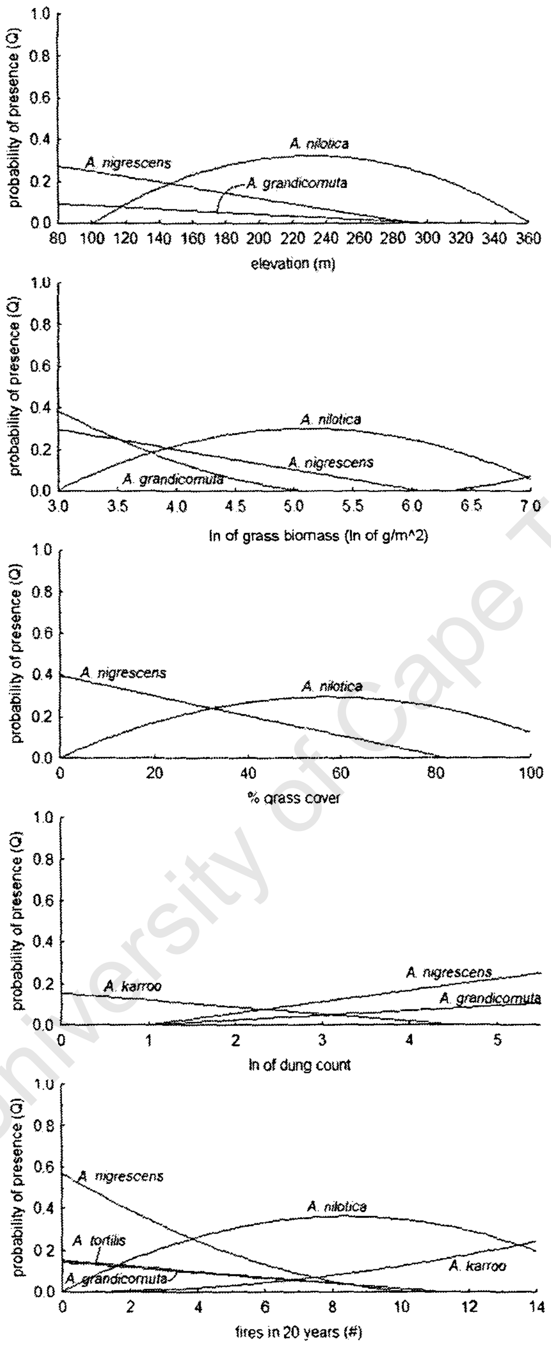

Figure 3.6. Probability of *Acacia* large tree occurrence along elevation, grass biomass, grass cover, dung count, and fire frequency gradients. Solid lines show linear or quadratic fits (see Table 3.3). Probability of large *Acacia* presence was less predictably related to gradients than *Acacia* sapling presence; significant patterns in adult distribution were similar to sapling distribution patterns.

Table 3.3. Probability of occurrence of large *Acacia* trees (ht $\geq$ 3.5m) along elevation, grass biomass, grass cover, herbivore pressure and fire frequency gradients. Polynomial regressions were done to define relationships between probability of occurrence (Q) of large *Acacia* trees and gradients. Only one large *A. caffra* was found, so this species was not analyzed.

Probability of small *Acacia* presence		R^2	p	fit equation
elevation	*A. gerrardii*		n.s.	
	A. karroo		n.s.	
	A. nilotica	0.642	0.0067	$Q = -0.69 + 0.0088*elev - 0.000019*elev^2$
	A. grandicornuta	0.498	0.015	$Q = 0. 13 - 0.00042*elev$
	A. nigrescens	0.604	0.0049	$Q = 0. 38 - 0.0013*elev$
	A. tortilis		n.s.	
grass biomass (g/m^2)	*A. gerrardii*		n.s.	
	A. karroo		n.s.	
	A. nilotica	0.788	0.045	$Q = -1.44 + 0.68*\ln(bm) - 0.067*\ln(bm)^2$
	A. grandicornuta	0.928	0.0091	$Q = 1.81 - 0.64*\ln(bm) + 0.056*\ln(bm)^2$
	A. nigrescens	0.871	0.0065	$Q = 0.59 - 0.097*\ln(bm)$
	A. tortilis		n.s.	
% grass cover	*A. gerrardii*		n.s.	
	A. karroo		n.s.	
	A. nilotica	0.668	0.049	$Q = 0.010*cover - 0.000091*cover^2$
	A. grandicornuta		n.s.	
	A. nigrescens	0.640	0.031	$Q = 0.40 - 0.0048*cover$
	A. tortilis		n.s.	
dung count (piles)	*A. gerrardii*		n.s.	
	A. karroo	0.671	0.0069	$Q = 0.15 - 0.034*\ln(dng)$
	A. nilotica		n.s.	
	A. grandicornuta	0.543	0.024	$Q = -0.021 + 0.023*\ln(dng)$
	A. nigrescens	0.531	0.026	$Q = -0.053 + 0.055*\ln(dng)$
	A. tortilis		n.s.	
# of fires in 20 years	*A. gerrardii*		n.s.	
	A. karroo	0.597	0.0012	$Q = 0.0012*fire^2$
	A. nilotica	0.427	0.025	$Q = 0.087*fire - 0.0052*fire^2$
	A. grandicornuta	0.500	0.0069	$Q = 0.14 - 0.013*fire$
	A. nigrescens	0.802	0.0001	$Q = 0.57 - 0.098*fire + 0.0041*fire^2$
	A. tortilis	0.575	0.0027	$Q = 0.15 - 0.014*fire$

Fire frequency was a more consistent predictor of probability of presence of *Acacia* adults (see Figure 3.6 and Table 3.3). Probability of presence of *A. karroo* adults increased with increasing fire frequency. Probability of presence of *A. grandicornuta*, *A. nigrescens*, and *A. tortilis* adults decreased with increasing fire frequency. *A. nilotica* adults occurred most frequently at intermediate fire frequency.

COMMUNITY ASSEMBLY AND CO-OCCURRENCE OF *ACACIA* SAPLINGS

Saplings - Ordination

NMDS ordination revealed that species were segregated along an axis correlated with grass cover, herbivore use intensity, and fire frequency (see Figure 3.7). Ordination resulted in a two-axis solution that fit original distances relatively well (R^2=0.518). Axis 2 was most correlated with grass cover (R^2=0.344), dung counts (R^2=0.341) and fire frequency (R^2=0.528). *A. karroo* and *A. caffra* saplings occurred at high grass cover, low dung counts, and high fire frequency. *A. nilotica* and *A. gerrardii* saplings were generalists that occurred at intermediate grass cover, dung counts, and fire frequency. *A. grandicornuta*, *A. nigrescens*, and *A. tortilis* saplings occurred at low grass cover, high dung counts, and low fire frequency. This analysis also suggests that *A. karroo* and *A. caffra* saplings likely co-occurred frequently, as well as *A. nigrescens* saplings with *A. tortilis* saplings.

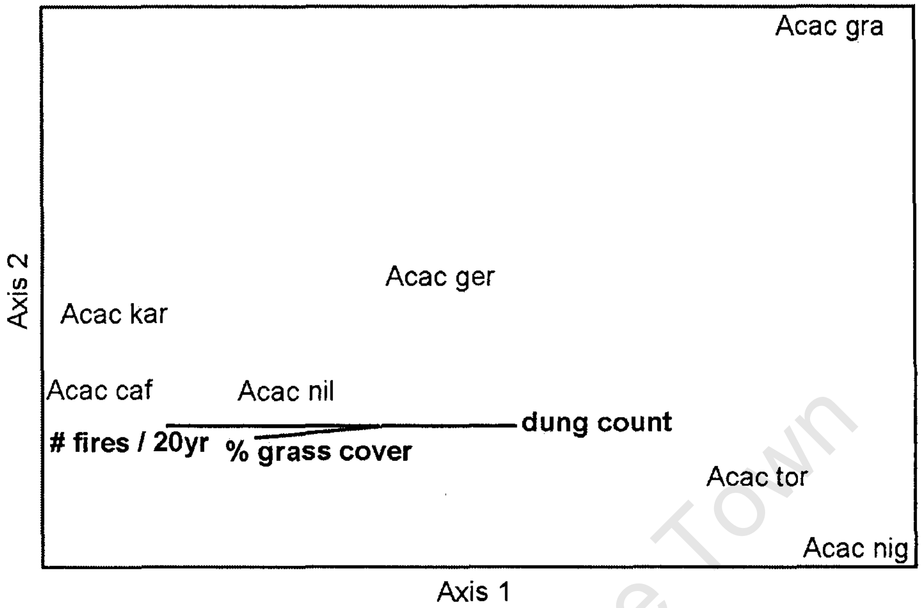

Figure 3.7. NMDS ordination of saplings of *Acacia* species. NMDS resulted in an ordination with a two axis solution, pictured here. Axis 1 was primarily related to grass cover (R^2=0.344), dung count (R^2=0.341) and number of fires in 20 years (R^2=0.528). These gradients had a major role in structuring species distributions and coexistence and defined a wide spread in species performance. Neither elevation – a surrogate for rainfall – nor grass biomass was correlated with either axis. However, the position of *A. grandicornuta* indicates that some other factor may also influence species coexistence.

Saplings – Null Model

We compared observed co-occurrence of saplings of *Acacia* species pairs with 1) totally random co-occurrence, and 2) co-occurrence along herbivory and fire gradients (see Table 3.4). Comparison of observed with random co-occurrence showed that species co-occurrence was not adequately explained by a random model. Species that co-occurred more frequently than expected were ecologically similar along herbivore use and fire frequency gradients; *A. karroo* and *A. caffra*, *A. karroo* and *A. nilotica*, *A. nigrescens* and *A. grandicornuta*, and *A. nigrescens* and *A. tortilis* saplings co-occurred more frequently than expected assuming random co-occurrence. Species that co-occurred less frequently than expected were ecologically dissimilar along grass, fire frequency, and herbivory gradients; *A. caffra* and *A. tortilis*, *A.*

Table 3.4. Observed versus expected co-occurrence of species-pairs using random and gradient-based co-occurrence models. χ^2 tests were used to determine whether differences between observed and expected plot distributions were different. The Dunn-Sidak modification of the Bonferroni correction was used ($\alpha = 1 - (1 - 0.05)^{1/c}$, where c is the number of comparisons) (Quinn & Keough 2002); a total of 21 species-pairs were compared ($\alpha = 0.0024$). '•' for no significance; '–' for exp < obs; '+' for exp > obs.

		A. caffra	*A.gerrardii*	*A. karroo*	*A. nilotica*	*A. grandicornuta*	*A. nigrescens*
random	*A. gerrardii*	•					
	A. karroo	–	•				
	A. nilotica	•	•	–			
	A. grandicornuta	•	•	+	+		
	A. nigrescens	•	•	+	•	–	
	A. tortilis	+	•	+	•	•	–
herbivore use	*A. gerrardii*	•					
	A. karroo	•	•				
	A. nilotica	•	–	•			
	A. grandicornuta	•	•	•	•		
	A. nigrescens	•	•	•	•	•	
	A. tortilis	•	•	•	•	•	•
fire frequency	*A. gerrardii*	•					
	A. karroo	•	•				
	A. nilotica	•	•	•			
	A. grandicornuta	•	•	•	•		
	A. nigrescens	•	•	+	•	•	
	A. tortilis	•	•	•	•	•	–

karroo and *A. grandicornuta*, *A. karroo* and *A. nigrescens*, *A. karroo* and *A. tortilis*, and *A. nilotica* and *A. grandicornuta* saplings co-occurred less frequently than expected assuming random co-occurrence (see Table 3.4).

Using herbivory and fire frequency gradients to predict rates of co-occurrence of saplings of species pairs resulted in substantially improved fit between expected and observed co-occurrence (see Table 3.4). When co-occurrence was predicted along the dung count gradient, observed and expected co-occurrence differed only for *A. gerrardii* and *A. nilotica* saplings. When co-occurrence was predicted along the fire frequency gradient, expected co-occurrence of *A. karroo* and *A. nigrescens* remained high, while expected co-occurrence of *A. nigrescens* and *A. tortilis* remained low. Co-occurrence calculated along herbivory and fire frequency gradients adequately predicted co-occurrence of all other species pairs.

SAPLING SPINESCENCE AND ARCHITECTURE

Acacia saplings had substantially different spinescence and branching architecture for all characters measured. Because variances were non-homogeneous and traits were not normally distributed, we used nonparametric Kruskal-Wallis ANOVAs to evaluate differences in traits among species. Species differed significantly in their density of primary branches per height (H=42.1, N=138, p<0.0001), density of secondary branches per height (H=20.8, N=138, p=0.0009), average spine length (H=57.3, N=137, p<0.0001), average spine width (H=60.5, N=138, p<0.0001), and average maximum leaf length (H=37.3, N=137, p<0.0001).

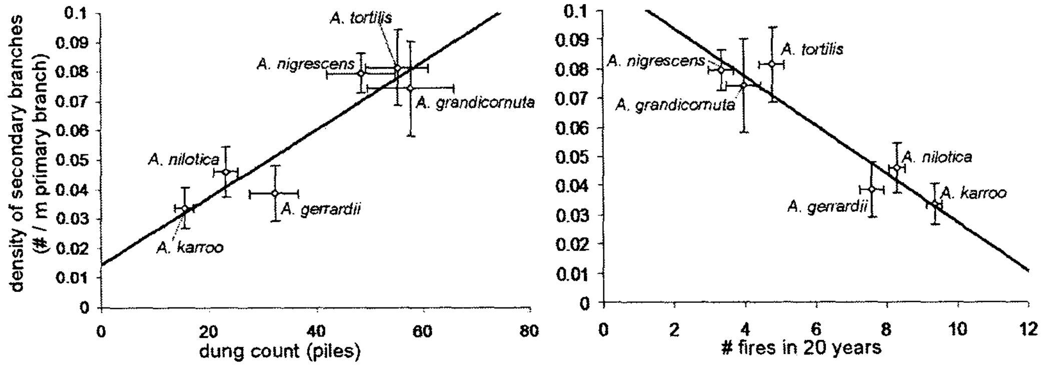

Figure 3.8. Density of secondary branches for each species versus mean grass biomass, grass cover, dung count, and fire frequency for plots where the species occurred. Error bars are standard error of means for each species. Degree of branching decreased with increasing grass biomass (R^2=0.841, p=0.010), grass cover (R^2=0.730, p=0.030), and increasing fire frequency (R^2=0.903, p=0.0036), but increased with increasing herbivore use intensity (dung count: R^2=0.859, p=0.0078). These patterns suggest that dense branching, or a 'cage' architecture, conferred an advantage in areas with intense herbivory and that sparse branching, or a 'pole' architecture, conferred an advantage in fire-prone environments.

However, only density of secondary branches was significantly related to mean grass biomass (R^2=0.841, p=0.010), grass cover (R^2=0.730, p=0.030), herbivore use (R^2=0.859, p=0.0078), and fire frequency (R^2=0.903, p=0.0036) (see Figure 3.8) for plots in which species were present. Secondary branching increased with increasing herbivore use and decreased as fire frequency and grass biomass increased. These patterns suggest that dense branching, or a 'cage' architecture, conferred an advantage in areas with intense herbivory and that sparse branching, or a 'pole' architecture, conferred an advantage in frequently burnt environments (see Figure 3.3).

Discussion

We examined community composition of the most common *Acacia* species in Hluhluwe iMfolozi Park in relation to rainfall (elevation), herbivore use, fire frequency, and grass biomass and cover. Herbivore use and fire frequency constitute direct disturbance gradients, while grass biomass and cover may affect trees directly, through resource competition, or indirectly, through their relation to fire and herbivory. We analyzed species distributions along these gradients (direct gradient analysis) and used ordination and a null-model to assess species co-occurrence patterns along the same gradients.

Distributions of saplings of most species were strongly related to fire, herbivory and grass gradients. *A. karroo* and *A. caffra* saplings co-occurred frequently and were most common in environments with high rainfall, frequent fire, low intensity herbivore use, and high grass biomass and cover. *A. grandicornuta* and *A. nigrescens* saplings also co-occurred frequently and were most common in environments with low rainfall, intense herbivory, low fire frequency, and low grass biomass. *A. tortilis* saplings were more common in environments with slightly higher grass biomass than *A. nigrescens* or *A. grandicornuta* saplings and were not constrained by rainfall, but nonetheless co-occurred frequently with *A. nigrescens* saplings. *A. gerrardii* appeared to be a true generalist, and co-occurrence with saplings of other species was random. *A. nilotica* was also a generalist but was most common in environments with intermediate herbivore use, intermediate grass biomass, and frequent fire.

These strong constraints on sapling distributions suggest that herbivores, fire and grass constrained *Acacia* species distribution by limiting sapling performance. Previous work has suggested that fire and herbivory, at least, limit tree establishment and help control savanna structure by imposing a demographic bottleneck on sapling recruitment into adults, and that saplings only mature when fire frequency or browsing pressure are relaxed (Prins & van der Jeugd 1993; Higgins *et al.* 2000; Chapters 4 & 6 in this volume). Saplings persist under high pressure from fire or herbivores until they are released, but persistence is only possible if saplings are able to survive this high pressure. This work suggests that saplings of different species of *Acacia* are able to survive different types of disturbances.

If fire and herbivory, together with grass biomass and cover, are able to constrain species distributions and limit growth of saplings into adults, variability in pressure from fire and herbivores allows saplings to escape and establish as adults (Prins & van der Jeugd 1993; Higgins *et al.* 2000). Fire, herbivory, and the grass layer are dynamic and variable savanna features (Coughenour 1991; Bailey *et al.* 1996; Schwinning & Parsons 1999; Balfour & Howison 2001; Archibald *et al.* 2005; D'Odorico *et al.* 2006). However, in this case, community composition was constant through time to some degree, at least at a broad spatial scale. Although disturbance gradients and grass communities were much less important in explaining distributions of adult *Acacia* trees than of saplings, adults of some species were structured along gradients, and those distributions were similar to distributions of *Acacia* saplings along the same gradients. In addition, covariation between fire frequency over the past 20 years and estimates of short-term herbivore use, grass biomass and grass cover from data collected in the field indicated that patches are relatively stable on this 20 year time scale. However, these features may not always be stable over longer periods (see Chapter 6); short-term changes in fire, herbivory, and grass on or within the landscape allow adult trees to establish and longer-term changes could potentially result in switches in composition from adult to sapling *Acacia* communities.

In fact, saplings of *A. karroo*, *A. nilotica*, and *A. tortilis* were frequently found even where conspecific adults were not present. Although saplings of all *Acacia* species were more often found where conspecific adults were present than where conspecific adults were not present, this frequent mismatch between saplings and adults suggests not only that dispersal may not have limited these species, but also that community composition may have been somewhat locally dynamic. Conversely, *A. grandicornuta* and *A. nigrescens* saplings occurred almost exclusively where conspecific adults also occurred. In the case of *A. nigrescens*, adults occurred with almost equal overall frequency to saplings, indicating that saplings are generally rare and recruitment may be declining (see also Chapter 6). In the case of *A. grandicornuta*, a close match between sapling and adult occurrence indicates that the heavily utilized grazing lawns on which this species occurred were fairly stable features of the savanna landscape. Frequent mismatches between distributions of saplings and adults of some *Acacia* species suggests that some landscape elements may be locally dynamic, while close associations between saplings and adults of other species suggests that other landscape elements, such as the most heavily utilized grazing lawns, may be relatively stable through time.

The species of *Acacia* considered in this study were clearly differentiated along disturbance and grass gradients. But can the location of a species along these gradients be predicted from plant functional traits? We investigated branching architecture and spinescence in *Acacia* saplings after Archibald and Bond (2003), who identified distinct growth forms in *A. karroo* in frequently burnt versus heavily browsed areas. *Acacia* saplings of different species varied in their branching structure. Secondary branching in particular was predictably related to gradients in fire, herbivory and grass cover, suggesting that species' architecture conferred adaptive advantages in the environments where they occurred. Species that occurred in areas of intense herbivory and infrequent fire were more branched, forming cages that may be a structural defense against herbivory (Marquis 1996; Stowe *et al.* 2000; Archibald & Bond 2003). Species that occurred where fires were frequent and herbivory less intense were less branched. Instead of branching, they invest in rapid vertical growth, which helps them reach a height at which they may no longer be as susceptible to damage from fire (Gignoux *et al.* 1997; Higgins *et al.* 2000; Archibald & Bond 2003).

Differentiation in branching architecture along fire and herbivory gradients, which can help saplings resist pressure from fire and herbivory, is additional evidence that fire and herbivory gradients were important in determining species' distributions and community assembly. Increasing ramification, from a pole-like to a cage-like architecture, along a gradient from frequently burnt to heavily grazed and browsed environments represented a trade-off for *Acacia* species in the type of disturbance they could survive. This clear trade-off between fire-adapted functional traits and herbivore adapted functional traits reflected differences in ecological niche use among these species of these *Acacia.*

Of note is the fact that spinescence did not vary predictably along a herbivore use gradient, although spines have been extensively discussed as structural defenses against herbivory (Gowda 1996; Gowda 1997). Degree of ramification, together with spines, may provide a better measure of whole-plant structural defense. Branching has been discussed as a browsing tolerance mechanism (Marquis 1996; Stowe *et al.* 2000) or even as a response to herbivory (Strauss & Agrawal 1999; Fornara & Du Toit 2007) instead of as a browsing avoidance mechanism. However, ramification is not always an induced trait (Cooper *et al.* 2003). A common garden experiment with seedlings of this suite of *Acacia* species in Hluhluwe iMfolozi Park showed that even as unbrowsed saplings, species exhibit the same predictable differences in architecture as we document here (Zululand Tree Project, unpublished data). We suggest that the formation of cages is an adaptive strategy for herbivore avoidance. This work certainly suggests that cage-formation may be a vital structural adaptation of *Acacia* saplings that occur in areas of intense herbivory; the possible role of architecture as a mechanism for *Acacia* avoidance of herbivory deserves more attention.

Differentiation of acacias along herbivore use, fire frequency, and grass gradients yields an ecologically diverse suite of species, with adaptations for success in diverse savanna systems. Covariation of grass biomass and cover gradients with herbivory and fire gradients makes it difficult to separate the effects of grass competition from the direct effects of herbivory and fire, but variation in architecture suggests that herbivory and fire are major determinants *Acacia* distribution.

Community assembly was not random across the landscape, and communities were organized according to fire frequency and herbivore use. Ecologically similar species, such as *A. caffra* and *A. karroo* or *A. grandicornuta*, *A. nigrescens* and *A. tortilis*, occurred together frequently. Contrary to traditional theoretical community ecology

(Connell 1961; MacArthur 1970; May & MacArthur 1972; Keddy & Shipley 1989; Chesson 2000; Tilman 2004), these co-occurrence patterns suggest that community assembly was regulated primarily via species' direct interactions with their environment, rather than via competition with each other.

Chapter 4

Browsing and a fire-grazer interaction: how herbivory influences tree populations in an African savanna

A. Carla Staver, William J. Bond, William D. Stock, Sue J. van Rensburg & Matthew S. Waldram

Introduction

'Top-down' disturbances in the form of fire and herbivory contribute to preserving the co-dominance of trees and grasses in savannas (Scholes & Archer 1997; Higgins *et al.* 2000; Sankaran *et al.* 2004; Sankaran *et al.* 2005). Acknowledging the defining role that fire and herbivory play in savannas marks a major shift away from implicitly equilibrium-based models that have traditionally dominated savanna ecology, such as Walter's root-niche separation hypothesis, in which trees and grasses are able to coexist because they do not directly compete for water (Walter 1971; Walker & Noy-Meir 1982). We now explicitly discuss savannas as dynamic systems. They are seldom in equilibrium with climate (Bond 2005; Bond *et al.* 2005; Sankaran *et al.* 2005), and tree-grass ratios fluctuate much more widely than equilibrium concepts allow, even over relatively short time periods (Walker *et al.* 1981; Westoby *et al.* 1989; Gillson 2004).

Fire is known to prevent large areas of savanna from reaching their maximum potential woody cover, as determined by climate (Bond 2005; Bond *et al.* 2005; Sankaran *et al.* 2005) and affects savanna structure and contributes to ecosystem heterogeneity (Eckhardt *et al.* 2000; Moreira 2000; van Wilgen *et al.* 2003; D'Odorico *et al.* 2006). Although fire has impacts on woody cover on landscape scales, Higgins *et al.* (2000) suggest that the mechanism is demographic at the tree population level. They suggest that fires limit woody cover by preventing establishment of adult trees (Hoffmann 1999; Higgins *et al.* 2000) rather than by killing existing adult trees. Fires are extremely damaging to tree saplings, often killing their shoots (Higgins *et al.* 2000; Hoffmann & Solbrig 2003), but rarely kill adults. Savanna tree saplings survive fire by storing starch in their roots (Hoffmann *et al.* 2003; Hoffmann *et al.* 2004), from which they resprout new shoots (Hoffmann 1998; Hoffmann *et al.* 2003). Saplings persist until they are afforded the opportunity to escape the 'fire trap' by growing into adult trees (Higgins *et al.* 2000; Gardner 2006). Though savanna saplings are thus equipped to survive fires, fire is thought to limit woody cover via a demographic bottleneck preventing the maturation of saplings to adults (Higgins *et al.* 2000).

Herbivory by large mammal herbivores has been more difficult to generalize. In part, the impacts of mammal herbivory depend on whether grazing or browsing predominates. In addition, mammal impacts depend on animal behavior—herbivores choose for often complex reasons where and when to feed (Coughenour 1991; Bailey *et al.* 1996)—and herbivores interact with other factors on the savanna landscape, including fire (Wronski 2003; Archibald *et al.* 2005; Zavala & Holdo 2005; Collins & Smith 2006).

Increases in woody plants resulting from intensive grazing have been reported frequently, especially in the rangeland literature (Archer 1990; van de Koppel *et al.* 1997; Roques *et al.* 2001; van Langevelde *et al.* 2003; Manier & Hobbs 2006). The phenomenon is usually attributed to less frequent less intense fires (Scholes & Archer 1997; van Langevelde *et al.* 2003; Archibald *et al.* 2005) but also to 'overgrazing' causing decreased tree-grass competition, favoring trees (Walter 1971; Walker & Noy-Meir 1982; Madany & West 1983), and even to herbivory aiding tree seed dispersal (Brown & Archer 1999). Grazing lawns are among the most heavily grazed components of a savanna system (McNaughton 1984). Paradoxically they typically have sparse tree cover. Lawns occur in savanna systems with native herbivores (Karki *et al.* 2000), particularly herd-forming herbivores (McNaughton 1984). Even in rangelands, cattle preferentially graze some areas more than others, creating grazing patches that can persist until cattle abandon them (Coughenour 1991; Schwinning & Parsons 1999).

In African savannas, the potential for top-down control of tree cover has long focused on the effects of megaherbivores, especially elephants, on large trees (Dublin *et al.* 1990; Bond & Loffell 2001; Baxter & Getz 2005; Birkett & Stevens-Wood 2005) and less on the impacts of smaller herbivores on tree population dynamics (Maron & Crone 2006). But browsing by meso- and mega-herbivores can suppress sapling growth (Barnes 2001; Augustine & McNaughton 2004; Sharam *et al.* 2006), and can even limit tree recruitment at the population level (Prins & van der Jeugd 1993). However, experimental work showing potential landscape level effects of herbivores on tree cover is lacking. In other systems around the world, browsers maintain open ecosystems by preventing saplings escaping to become trees. In Yellowstone National Park, high elk density is thought to account for low levels of recruitment of quaking aspen, *Populus tremuloides* (Romme *et al.* 1995; Ripple *et al.* 2001). White-tailed deer suppress growth and recruitment of hemlock, *Tsuga canadensis*, in the northern Great Lakes Region of the United States (Rooney *et al.* 2000). In Europe, mixed feeders red deer and chamois may limit recruitment of the European silver fir, *Abies alba* (Weisberg & Bugmann 2003). The domestic goat, another mixed feeder, is notorious for its effects on sapling growth and recruitment of woody plants (Stuart-Hill 1992; Hester *et al.* 2006).

In African savannas, the potential for medium and large herbivores to limit woody cover is complicated by fire. Herbivory includes browsing, which impacts the tree layer directly, and grazing, which interacts with fire. How do these aggregate on the landscape? And can we suggest, based on which demographic processes are most affected, the ways in which herbivory may contribute to savanna structure?

This paper reports a study of the effects of herbivory by medium and large mammals on *Acacia* demography in a savanna in KwaZulu Natal, South Africa. *Acacia* species are dominant in the area, including *A. nilotica*, *A. karroo*, *A. gerrardii*, *A. nigrescens*, and *A. tortilis*, and saplings especially are preferred and heavily utilized by herbivores. A series of herbivore exclosures was erected in 1999 to exclude medium and large mammals and vegetation responses were recorded over a period of six years. Sites were selected in a mesic and a semi-arid savanna and in heavily-grazed lawn and lightly-grazed bunch-grass areas in each to determine whether the effects of herbivory by large mammals are context-dependent. Fires are frequent in these savannas. Our study included consideration of both herbivory and fire and their interactive effects on *Acacia* demography.

Study Area

The study was conducted in Hluhluwe iMfolozi Park (900 km^2; 28°00' – 28°26' S; 31°43' – 32°09' E), located in northern KwaZulu Natal, South Africa. Topography is varied, consisting mainly of rolling hills of up to 540m elevation in the Hluhluwe Game Reserve area falling into broader river valleys at 40m elevation in the iMfolozi Game Reserve area. Soil types are closely linked to bedrock geology (Graham 1992), consisting predominantly of shales and sandstones with intermittent doleritic intrusions (King 1970; Graham 1992). Because slopes are steep, catenary sequences that dominate soils in other African savannas are not distinct in this area (Graham 1992). Experimental sites were located on dolerite- and sandstone-derived soils, with some shales, in Hluhluwe Reserve and on dolerite-derived soils in iMfolozi Reserve.

Rainfall is closely linked to elevation within the park (Balfour & Howison 2001), producing a rainfall gradient between higher elevation Hluhluwe GR and lower elevation iMfolozi GR. Although the ten sites selected for this study are located in areas of Hluhluwe and iMfolozi reserves with similar elevation (between 171m and 305m in Hluhluwe and 116m to 265m in iMfolozi), Hluhluwe sites generally receive more rain (~720mm per year) than iMfolozi sites (~655mm per year), both mostly during the summer. From a long-term rainfall monitoring station at Hilltop Tourist Camp in Hluhluwe, the study included above- and below-average years. A maximum rainfall of 983 mm fell during the 2003/2004 season and a minimum of 694 during the 2004/2005 season; average annual rainfall at Hilltop Camp was 974 mm between 1933 and 2006. Hluhluwe daily temperatures range between ~39°C (mean daily T_{max}) and ~15°C (mean daily T_{min}) in summer and between ~32°C and ~9°C in winter. iMfolozi daily temperatures range between ~40°C and ~14°C in summer and between ~34°C and ~6°C in winter (Zululand Tree Project baseline data).

The two reserves constitute ecologically distinct areas characterized by different plant species composition and fire frequency and large mammal herbivore pressure. Most areas in the Hluhluwe Reserve, including areas of relatively low rainfall, have burned more than 10 times between 1956 and 1996, while most areas in the iMfolozi Reserve have burned only between one and eight times during the same period (Balfour & Howison 2001). Large mammal herbivore densities within and between reserves vary depending on herbivore habitat preferences. Impala (*Aepyceros melampus*) are by far the most numerous herbivore in the park and occur with higher densities in semi-arid iMfolozi (36 per km^2) than in mesic Hluhluwe (24 per km^2); white rhino (*Ceratotherium simum*) make up the largest biomass in the park with higher densities in iMfolozi (2.5 per km^2) than Hluhluwe (1.8 per km^2). Herbivore densities have fluctuated substantially during the past century in Hluhluwe iMfolozi Park, largely due to hunting, the rinderpest epidemic, and culling campaigns during the early part of the 20th century associated with efforts to eradicate the *nagana* livestock disease. In 1929, impala, giraffe (*Giraffa camelopardalis*), and elephant (*Loxodonta africana*) were extinct in both Hluhluwe and iMfolozi Reserves; white rhino in Hluhluwe and nyala (*Tragelaphus angasi*) in iMfolozi were also eliminated (Mentis 1968). These species have all been re-introduced in the last half century. However, herbivore densities have recuperated and have been dramatically higher during the last 20 years than at any point during the preceding century. The park currently employs drought mitigation strategies, including limiting fire during dry periods and controlling animal populations, to minimize widespread death of game from drought.

Methods

TREATMENTS

Five sites each were selected in a mesic (Hluhluwe) and a semi-arid savanna (iMfolozi), three in high herbivore-pressure grazing lawns and two in low herbivore pressure bunchgrass areas. Sites were selected in open areas with low adult tree densities. In 1999 at each site, we set up three herbivore exclusion treatment plots of 40m x 40m. The control (all herbivores = 'all') allows access to all herbivores, a cable set 70cm above the ground excludes rhinos (rhino fence = '- rhino'), and a mesh fence excludes hares (*Lepas saxatilis*) and all larger herbivores (total exclosure = '- all') (see Figure 4.1). Dung was counted every month during the study period to verify herbivore exclusion treatments.

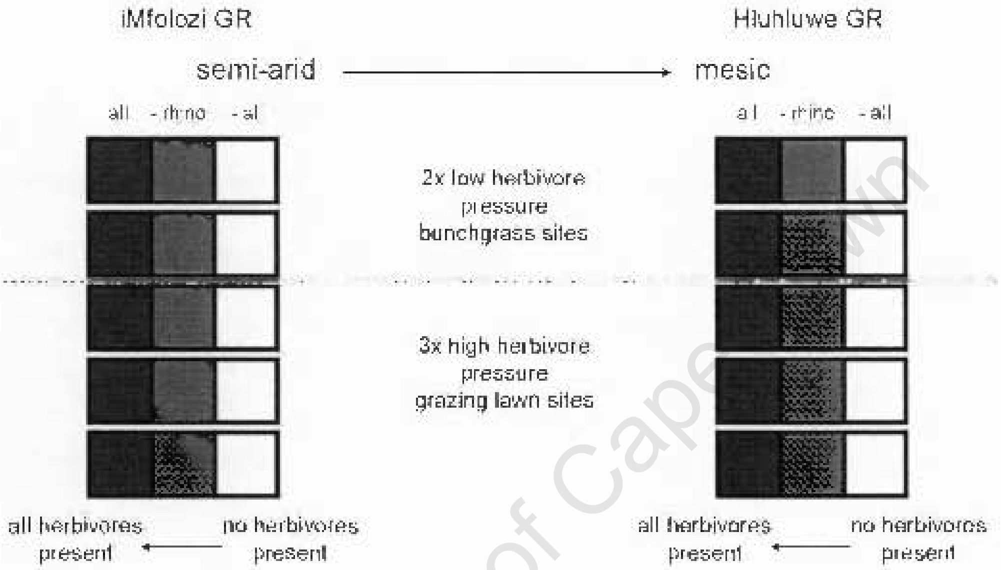

Figure 4.1. Experimental design of herbivore exclosures. Two parks (mesic Hluhluwe and semi-arid iMfolozi GR), two bunchgrass sites each and three grazing lawn sites each, with three exclusion treatments at each site. Treatment notation used throughout: 'all' = control with all herbivores present, '– rhino' = rhino and larger herbivores excluded via a single low cable fence, and '– all' = all mega- and mesoherbivores excluded.

Half of each plot, or treatment, was divided into a permanent 2m x 2m grid, onto which all woody plants were mapped and their heights recorded in 2000, after plots were established. They were relocated and their heights measured after the end of each growing season). New individuals were recorded during each census and tracked thereafter. We have excluded the first census, for 2000, because of problems standardizing methods and effects.

All sites were burnt during the dry seasons of 2000, 2002, and 2004, a two year fire return interval. Sites and treatments that sustain high grass biomass burnt readily, while heavily grazed areas often did not burn. At all sites the complete exclosure treatment generated sufficient grass biomass to burn the whole plot. Thus complete herbivore exclusion was always associated with exposure of saplings to fire.

ANALYSIS

We have pooled all *Acacia* species found in each of the treatment plots. *Acacia* species distribution is not even throughout the park, although there are a few dominant species. This makes analyzing any one species across all sites impossible. However, annual growth in plant height (discussed below) does not differ consistently among species ($F=1.31$, $df=7$, $p=0.25$); differences among bunchgrass/grazing lawn, fire, and herbivore exclusion treatments are bigger and more consistent, as discussed in the results section.

We have focused on three demographic processes: seedling establishment, sapling growth (where a sapling is an acacia $\leq$ 200cm), and sapling mortality. Because they are small, seedlings and saplings are most vulnerable to browsing by antelope and most susceptible to topkill in fires.

- Establishing seedlings were defined as new individuals recorded in at least two successive years. Seedling height is presented as the average height of emerging seedlings per plot and seedling establishment as the total number of seedlings per plot.
- Sapling growth was defined as the change in height of an individual from one year's census to the next and can be negative. All saplings (ht $\leq$ 200cm) appearing in the two consecutive censuses are included. We considered dividing saplings into smaller

and larger saplings, but abandoned the idea because growth is not related to initial sapling size as might be expected (r^2=0.011, p=0.0039).

- Sapling mortality was calculated for each plot. A dead individual is defined as an individual that was absent in two successive growing seasons.

We also examined height of the biggest saplings (top 20%) after a growing season; these individuals are most likely to grow into adults and better reflect the effects of fire and herbivory than mean values.

Repeated measures analysis of variance was used with two or four years of data, categorized into 'fire' or 'no fire' years. We examined effects of fencing treatment (large herbivore exclusion) and initial herbivore pressure (bunchgrass=low, grazing lawn=high) on seedling establishment and seedling height, and sapling growth, height, and mortality in each plot. STATISTICA V6 was used for statistical data analysis (StatSoft 2004).

We analyzed treatment effects on sapling growth data in years when plots had burned (2002-2003 and 2004-2005) and in years when they had not (2001-2002 and 2003-2004). Seedling height, seedling establishment, and sapling mortality were compared for years with (2002-2003) and without fire (2001-2002).

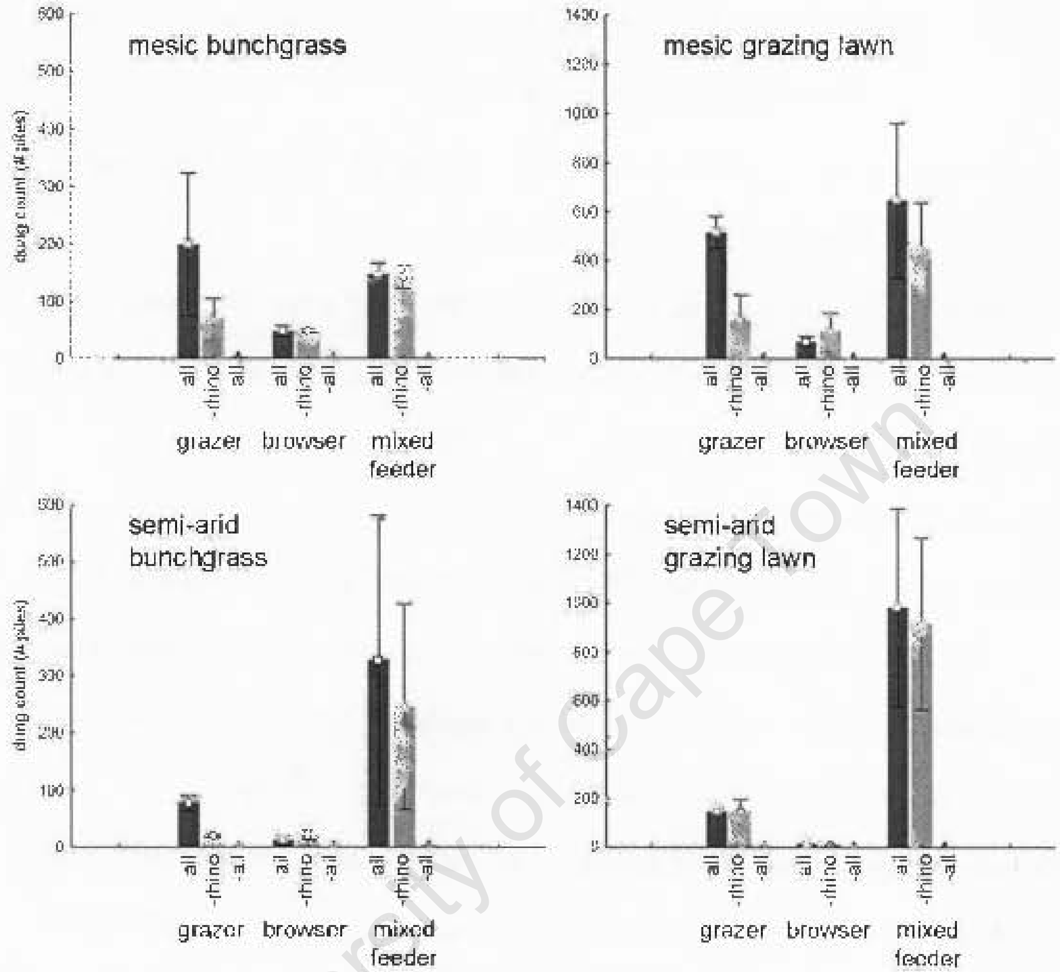

Figure 4.2. Effects of exclusion treatment on herbivore dung counts. Note differences in axis scale between bunchgrass areas (left) and grazing lawns (right). Vertical lines represent standard error of means. Dung presence and abundance were recorded on a monthly basis in all treatments from 2001 to 2005 to verify that fencing does constitute herbivore exclusion. Partial ('- rhino') exclusion resulted in reductions in grazer pressure but little to no reduction in browser and mixed-feeder use; total herbivore exclusion ('- all') eliminated large mammal herbivores completely.

Results

Herbivore exclosures were effective and strongly influenced herbivore use of treatment plots (Figure 4.2). Partial ('- rhino') exclusion resulted in reductions in grazer pressure but little to no reduction in browser and mixed-feeder use; total herbivore exclusion ('- all') eliminated large mammal herbivores completely. Mixed feeders, which include impala and nyala in Hluhluwe iMfolozi Park, dominated dung counts. Thus herbivore exclusion resulted in reductions in both grazing and browsing.

EFFECTS OF LARGE HERBIVORE EXCLUSION AND FIRE

Mesic Savanna in Hluhluwe

Herbivore exclusion did not consistently impact seedling establishment or seedling height in mesic Hluhluwe (see Table 4.1). Fire affected seedling establishment and reduced seedling height, but these effects were variable across treatments. Seedling height and in particular seedling establishment varied widely across treatment and site, with no clear differences among treatments or among grazing lawn and bunchgrass sites, indicating that some other factor was controlling seedling establishment. Mean seedling height was 34.7 cm, and seedling height ranged between 12cm and 69cm; mean seedling establishment per plot per year was 8.6 seedlings, and seedling establishment ranged between 0 and 23 per plot.

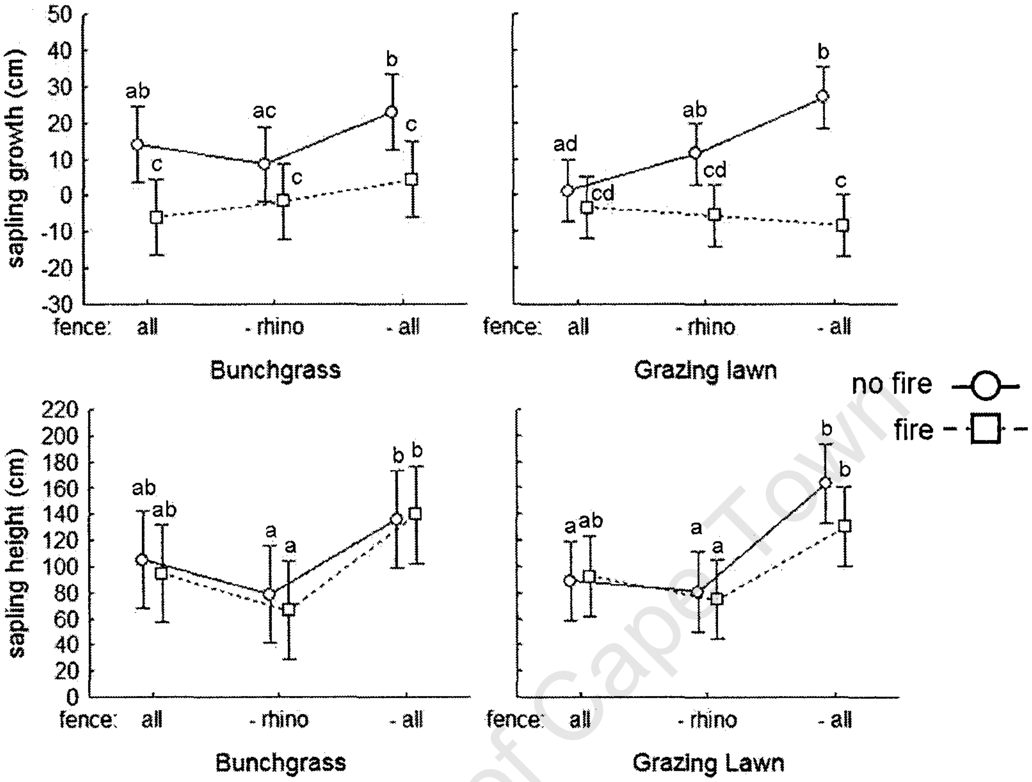

Figure 4.3. Effects of exclusion treatment in mesic Hluhluwe Reserve on annual sapling height growth and post-growing season height of successful saplings (top 20%). Vertical bars represent 95% confidence intervals on means. Sapling growth increased significantly with herbivore exclusion in bunchgrass and grazing lawn areas, and the effects of fire were more substantial as herbivores were excluded, particularly on grazing lawns. Increased growth translated into larger size of the largest saplings most likely to grow into adults. Thus, although browsing and the fire-grazer interaction were different in bunchgrass and lawns grass areas, herbivory had an important role in limiting sapling success in both systems.

Herbivore exclusion resulted in increased sapling growth both in grazing lawns and slightly less in bunchgrass areas (see Figure 4.3; Table 4.1). In grazing lawns, differences between fire-year and no-fire-year sapling growth were bigger in exclosures. However, although grazer exclusion resulted in increased fire effects, browser exclusion nonetheless resulted in increased sapling growth. In bunchgrass areas, there was no change in the effects of fire on sapling growth in exclosures. Thus, grazers had little effective impact on bunchgrass fuel loads and fire intensity, but browsers had substantial impacts on sapling growth. Aggregated over two years, herbivore exclusion substantially

Table 4.1. Results of repeated measures ANOVA. Fence denotes herbivore exclusion treatment; fire denotes fire v. no fire years; hp denotes bunchgrass areas v. grazing lawns; region denotes mesic v. semi-arid savanna.

	fence			Fire			fire*fence			fire*hp*fence			region*fire*hp* fence		
	F	*df*	*p*	*F*	*df*	*p*	*F*	*Df*	*p*	*F*	*df*	*p*	*F*	*df*	*p*
seedling establishment															
Hluhluwe	4.0	2	0.058	78.4	1	<0.0001	12.8	2	0.0023	9.7	2	0.0056	0.76	2	0.48
iMfolozi	1.5	2	0.28	0.53	1	0.48	1.8	2	0.22	2.2	2	0.16			
seedling height															
Hluhluwe	2.2	2	0.16	67.1	1	0.014	1.4	2	0.29	0.06	2	0.93	2.7	2	0.095
iMfolozi	3.9	2	0.059	0.08	1	0.78	0.05	2	0.95	0.24	2	0.79			
sapling growth – 1 yr															
Hluhluwe	10.8	4	0.0002	17.8	2	0.0011	1.5	4	0.23	4.7	4	0.011	4.6	4	0.0043
iMfolozi	1.1	4	0.38	54.2	2	<0.0001	0.74	4	0.58	4.3	4	0.015			
sapling mortality															
Hluhluwe	0.82	2	0.47	0.001	1	0.76	0.007	2	0.51	0.005	2	0.59	1.6	2	0.23
iMfolozi	0.68	2	0.53	0.05	1	0.091	0.06	2	0.058	0.001	2	0.92			
sapling height															
Hluhluwe	5.1	4	0.0078	13.4	2	0.0028	1.6	4	0.22	1.5	4	0.24	1.4	4	0.26
iMfolozi	2.7	4	0.068	8.3	2	0.011	4.9	2	0.04	0.83	4	0.53			
sapling height – top 20%															
Hluhluwe	8.76	4	0.0006	7.19	2	0.016	0.83	4	0.53	1.96	4	0.15	1.1	4	0.37
iMfolozi	1.59	4	0.22	11.0	2	0.0050	0.53	4	0.71	0.53	4	0.72			

	fence			Hp			hp*fence			region*fence			region*hp*fence		
	F	*df*	*p*	*F*	*df*	*p*	*F*	*Df*	*p*	*F*	*df*	*p*	*F*	*df*	*P*
sapling growth – 2 yr															
Hluhluwe	10.8	4	0.0002	8.3	2	0.011	1.2	4	0.037	3.7	4	0.013	0.71	4	0.59
iMfolozi	1.1	4	0.38	0.26	2	0.78	0.26	4	0.90						

increased growth in both grazing lawns and bunchgrass areas (see Figure 4.4; Table 4.1). As a result, the biggest saplings were ~60cm taller inside total exclosures than outside (see Figure 4.3; Table 4.1; Figure 4.5). Thus, although browsing and the fire-grazer interaction were different in bunchgrass and lawn grass areas, herbivory had an important role in limiting sapling growth in both systems.

Only initial herbivore pressure had any effect on sapling mortality (see Table 4.1); more saplings died in bunchgrass areas than on grazing lawns. There were no significant effects of fire or herbivore exclusion on sapling mortality over six year study period. Mean sapling mortality was 24.9%, and mortality ranged between 0% and 68%, although most plots had mortality less than 20%.

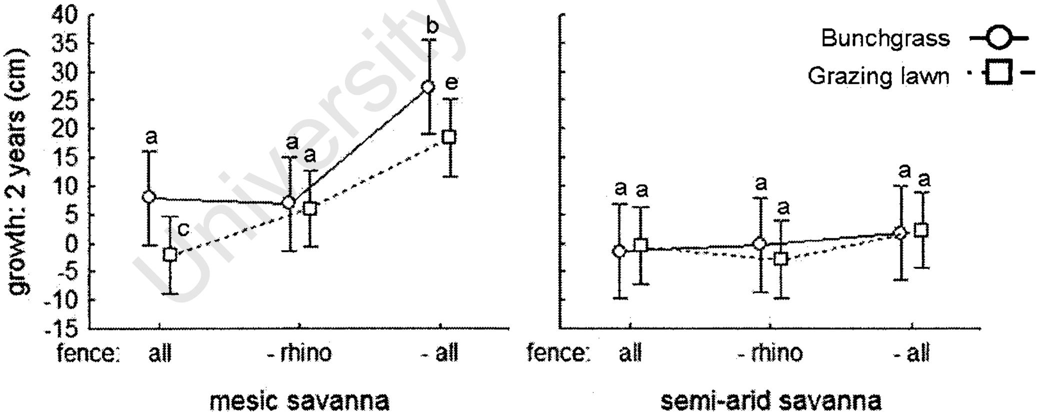

Figure 4.4. Effects of exclusion treatment on net sapling growth over two years, including a fire- and a no-fire-years. Vertical bars represent 95% confidence intervals on means. In the mesic savanna, browsing had clear effects on sapling growth in both grazing lawns and bunchgrass areas that were bigger than the effects of increasing fire intensity with grazer exclusion. In the semi-arid savanna, sapling growth responded to herbivore exclusion neither in bunchgrass areas nor in grazing lawns, although browsing and fire effects were different in these areas.

Figure 4.5. Examples of grazing lawn (left) and bunchgrass (right) sites in the mesic (top) and semi-arid (bottom) savannas. Control areas with all herbivores present are pictured in the foreground and total herbivore exclosures in the background. Herbivory had major impacts on sapling size in both grazing lawns and bunch grasslands in the mesic savanna and no impact on sapling size in either in the semi-arid savanna. In grazing lawns in both mesic and semi-arid savannas, herbivory had major impacts on grass biomass and herbivore exclusion resulted in increased grass biomass, but not in bunchgrass areas.

Semi-Arid Savanna in iMfolozi

Neither herbivore exclusion nor fire affected seedling establishment or seedling height in iMfolozi sites (see Table 4.1). Both seedling establishment and seedling height varied substantially among sites, indicating, as in mesic Hluhluwe, that some other factor may have been controlling seedling establishment and height. Mean seedling height was 21.2 cm, ranging from10cm to 60cm; mean seedling establishment per plot per year was 6.4 seedlings, ranging from 0 to 94 seedlings per plot.

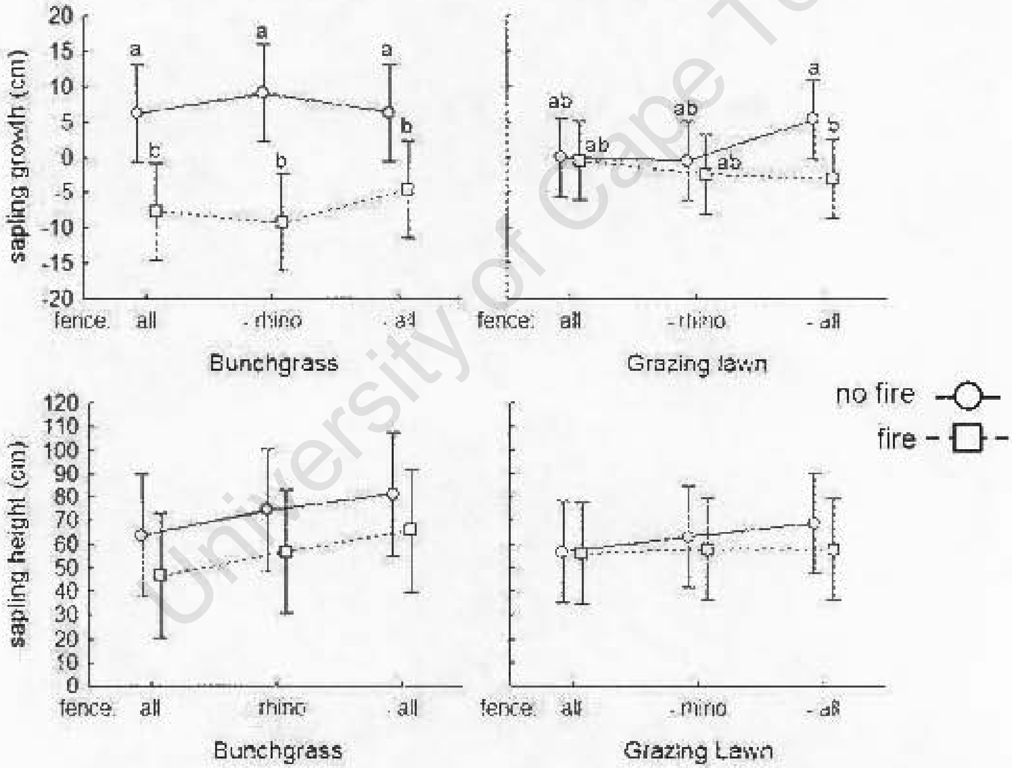

Figure 4.6. Effects of exclusion treatment in semi-arid iMfolozi Reserve on annual sapling height growth and post-growing season height of successful saplings (top 20%). Vertical bars represent 95% confidence intervals on means. Sapling growth increased significantly with herbivore exclusion in grazing lawns only, where the effects of fire increased with grazer exclusion. Sapling growth did not change with herbivore exclusion in bunchgrass areas, but fire had clear effects on growth. In neither bunchgrass areas nor grazing lawns did changes in growth translate into larger size of the largest saplings most likely to grow into adults. Thus, although browsing and the fire-grazer interaction were clearly different in bunchgrass and lawns grass areas, herbivory seemed to be of limited importance in controlling sapling success in both systems.

Herbivore exclusion resulted in increased sapling growth only on grazing lawns, where differences between fire-year and no-fire-year growth were bigger in exclosures (see Figure 4.6; Table 4.1). As in mesic grazing lawns, the complete exclosure resulted in browser exclusion and in increased sapling growth but also in grazer exclusion with increased fire effects reducing growth. However, unlike in mesic Hluhluwe, herbivore exclusion in bunchgrass habitats did no affect sapling growth; only fire clearly decreased sapling growth. Aggregated over two successive censuses, including a fire then a no-fire year, herbivore exclusion had no effect on sapling growth in either grazing lawns or bunchgrass areas (see Figure 4.4; Table 4.1). Herbivore exclusion also had no effect on sapling height (see Figure 4.6; Table 4.1; Figure 4.5). Thus, although browsing and the fire-grazing dynamic were substantially different in bunchgrass and lawn grass areas, herbivory seemed to be of limited importance in controlling sapling success. In general, sapling growth was substantially less in semi-arid iMfolozi (maximum ~15cm per year) than in mesic Hluhluwe (maximum ~30cm per year) (F=31.1, df=2, p<0.0001).

No factor included in this study had any impact on sapling mortality (see Table 4.1). Mean mortality was 22.6%, and mortality ranged between 0% and 50%, although most plots had mortality less than 30%.

Discussion

We have examined the possible effects of herbivory on tree population dynamics by testing the effects of herbivore removal on seedling and sapling life stages, which are the life-stages most vulnerable to the effects of both herbivory (Roques *et al.* 2001) and fire (Hoffmann 1999; Higgins *et al* 2000). We have explicitly considered the direct effects of browsing on seedlings and saplings and also the indirect effects of increased fire intensity resulting from increasing grass fuel loads with grazer removal.

A BROWSER-INDUCED DEMOGRAPHIC BOTTLENECK?

Large mammal herbivores can clearly have a major impact on savanna tree cover by suppressing growth of *Acacia* saplings to near zero in systems like Hluhluwe iMfolozi Park with relatively high herbivore densities. These impacts were on sapling growth rather than on seedling establishment or sapling mortality. Seedling establishment varied, but the major differences in number of seedlings were not predictably related to herbivore exclusion, fire intensity, or bunchgrass/grazing lawn differences. Others have suggested that variation in seedling establishment is a spatial process (Smith & Goodman 1987; Couteron & Kokou 1997) that may be more strongly related to another factor not included here, such as dispersal (Brown & Archer 1999) and temporal rainfall variability (O'Connor 1995; Stave *et al.* 2006). Shaw *et al.* (2002) suggest that seedling establishment and height may be more closely related to invertebrate and rodent herbivory than to herbivory by meso- and megaherbivores. However, seedling establishment may not be a significant demographic limitation in our study area. Densities of saplings averaged 824 per hectare in the mesic savanna and 590 per hectare in the semi-arid savanna. These sapling densities would result in closed woodlands (defined as having tree densities of between 200 to 400 trees per hectare) if all saplings escaped fire and browsing to grow into trees.

Sapling mortality varied even less, although slightly better survivorship in grazing lawns than in bunchgrass areas indicated that higher intensity fires may lead to mortality over a longer period than this six year study.

By far the most important impact of large mammal herbivores was on sapling growth. Saplings are stuck in a 'browse trap', a demographic bottleneck analogous to the 'fire trap' outlined in Higgins *et al.* (2000), in which herbivores suppress transition of saplings into young adults while not affecting escaped adult trees. Saplings persist in the browse or fire trap until they are released and can mature. Thus, like fire, browsing in this natural savanna strongly favors grass in the tree-grass ratio. So how do trees persist, given intense pressure from herbivores or fire? Though both limit opportunities for saplings to escape the trap and grow into adults, the browse trap differs from the fire trap because herbivory applies more continuous and less intense pressure, until herbivore pressure is reduced, allowing saplings to grow.

Episodic reductions in herbivore pressure would allow trees to escape the 'browse trap' in systems with native herbivore assemblages. Reductions in browse pressure may arise for numerous reasons including drought and disease (Young 1994; Gaillard *et al.* 1998; Owen-Smith & Ogutu 2003), seasonal shifts in diet composition (Sponheimer *et al.* 2003), and local changes in herbivore pressure when patch selection by mixed feeders changes (Coughenour 1991; Bailey *et al.* 1996). For instance, the major large tree establishment events in Lake Manyara Park in Tanzania resulted directly from repeated anthrax outbreaks in impala (Prins & van der Jeugd 1993). Schwinning and Parsons (1999) argue that herbivory is highly variable both spatially and temporally, negating the assumption of continuity and homogeneity in herbivore ecology. This variability would be essential for sapling release from a 'browse trap'.

LANDSCAPE CONTEXT AND THE FIRE-GRAZER INTERACTION

The impacts of herbivory on sapling growth and height were not uniform across the savanna and depended on landscape context. In the mesic savanna, browsing had major impacts on sapling growth and height in both bunch and lawn grass sites. However, on grazing lawns, grazer exclusion caused increases in fire intensity, but fire was insufficient to offset increases in sapling growth with browser removal. Thus, herbivore exclusion had a net positive effect on sapling growth and height regardless of local herbivore pressure throughout the mesic savanna landscape. In the semi-arid savanna, browsing impacted sapling growth only in grazing lawns, where local herbivore pressure is highest. Fire intensity increased with grazer exclusion and fully offset the effects of browser exclusion. Thus, herbivore exclusion had no net effect on sapling growth or height in any part of the semi-arid savanna landscape. Rainfall broadly determined whether browsers were able to effectively suppress saplings, although differences in browsing and grazing-fire interactions on a local scale probably play a role in determining what factors result in a sapling 'release event'.

Although the effects of herbivory are less visually apparent in mesic savannas than they are in semi-arid savannas, browsing may be a vital determinant in limiting tree cover in these areas. Higher rainfall promotes grass productivity, higher fuel loads, and more frequent and intense fires in the bunch grasslands of the mesic savanna. Yet fire alone was insufficient to suppress saplings. Both fire and browsing were necessary to suppress sapling growth and control tree recruitment. The potential role of browsing in limiting tree cover in semi-arid savannas is less clear. Browsing can clearly limit sapling growth on grazing lawns, where a reduction in browse pressure would usually be associated with a reduction in grazing, increased grass fuel loads and higher fire risk. Slow sapling growth rates and the interaction between grazers and fire make escape unlikely. However, these effects occur in a dynamic and heterogeneous savanna landscape; if reductions in herbivore pressure are localized, even areas with increased fuel loads may experience long fire return intervals. Alternatively, rainfall and rainfall variability may also play a major role in limiting tree growth in semi-arid savannas (e.g. Miller *et al.* 2001) and in providing opportunities for trees to escape from browsing and fire pressure. However, this study was conducted during a five-year period that included above- and below-average rainfall years. Saplings in the semi-arid savanna were nonetheless unable to escape.

Conclusions

We suggest that 'top-down' disturbances from herbivory may be an important control on tree cover in savannas, both through the direct impact of browsing on sapling and through the competition of grazers with fire for grass. We found no indication that heavy grazing pressure promotes tree growth by reducing competition from grasses.

Browsing can suppress sapling growth and may thereby prevent transition from sapling to adult life stages. This 'browse trap' can limit large tree emergence, but saplings may be able to escape during times of low herbivore pressure. Thus variability, both spatial and temporal, defines *Acacia* population dynamics. Browsing can suppress tree growth even in areas of low herbivore pressure, however, which suggests that the effects of browsing may contribute to limiting tree cover on a landscape scale as well as in heavily utilized patches.

Trade-offs between intense grazing, often associated with intense browsing, and fire intensity and frequency also impact on sapling growth. In high rainfall areas, grazing rarely excludes fire, and browsing and fire together are necessary to limit the emergence of trees. A release from either may result in a sapling release event, and events may occur frequently. In low rainfall areas, browsing or fire alone is sufficient to limit sapling growth. Only the simultaneous reduction of browsing and fire or an increase sapling growth rates would allow saplings to escape and become large trees, and events may be rare. In this way, rainfall probably defines the interaction between fire and herbivory, and affects trees response to changes in disturbances from herbivory and fire. We suggest that consumers, including herbivory as well as fire, are instrumental in limiting woody cover and in maintaining the coexistence of trees and grass in these systems.

Chapter 5

Age determination of three African *Acacia* species using ring-counts and ^{14}C dating

A. Carla Staver, Edmund C. February, & William J. Bond

Introduction

The inability to accurately and easily estimate tree ages and growth rates in the tropics and sub-tropics imposes limitations on our ability to examine tree population dynamics (Ashton 1981; Belsky & Canham 1994; Terborgh *et al.* 1997; Higgins *et al.* 2000). Savannas in particular are subject to major disturbances from fire, herbivory, and variable climate that admit the co-dominance of trees and grass (Westoby *et al.* 1989; Scholes & Archer 1997; Sankaran *et al.* 2004; Sankaran *et al.* 2005), and a better understanding of tree population dynamics has the potential to contribute significantly to our understanding of savanna functioning. However, although fire, herbivory, and variable climate are now discussed as drivers of non-equilibrium savanna ecosystems, studies that explicitly consider tree population dynamics in this context are few. These have relied on uncalibrated age estimation by tree rings (Prins & van der Jeugd 1993) or on long-term aerial photography (Archer *et al.* 1988; Brown & Archer 1999), which is unavailable in many areas and which can only roughly approximate population dynamics.

Dendrochronology is widely assumed to be impossible in areas without significant temperature seasonality (Belsky & Canham 1994). However, the formation of tree rings arising from rainfall seasonality has been documented for tropical and sub-tropical areas around the world (see Mariaux 1981; Détienne 1989; Jacoby 1989; Vetter & Botosso 1989; Worbes & Junk 1989; Worbes 1999; Fichtler *et al.* 2003; Grau *et al.* 2003; Brienen & Zuidema 2005; Brienen & Zuidema 2006), although these rings often cannot be counted (Martin & Moss 1997). In Africa, species of the diverse and widespread *Acacia* form bands of marginal parenchyma related to the beginning or end of the rainy season that can be counted to give a reasonable approximation of tree age (Gourlay & Kanowski

1991; Wyant & Reid 1992; Prins & van der Jeugd 1993; Gourlay & Grime 1994; Gourlay 1995; Gourlay *et al.* 1996; Martin & Moss 1997; February *et al.* 2006). Efforts to validate the use of these marginal parenchyma bands have used cambial injury studies (Wyant & Reid 1992), which are limited by their necessarily short time span, or tree rings counts using trees of known age (Gourlay & Kanowski 1991) or trees which have been radiocarbon dated (February *et al.* 2006). These studies have generally been limited to few trees (Gourlay & Grime 1994; Gourlay 1995; February *et al.* 2006) or to trees similar in age (Gourlay & Kanowski 1991; Martin & Moss 1997). Here we report an attempt to generalize a relationship between ages from ring counts and radiocarbon age for three *Acacia* species (*A. karroo*, *A. nilotica*, and *A. nigrescens*). The primary objective was to develop a method to determine the ages of trees from ring counts in order to better understand tree population dynamics in savanna systems.

Methods

The study was conducted in Hluhluwe iMfolozi Park (900 km^2; 28°00' – 28°26' S; 31°43' – 32°09' E) in northern KwaZulu Natal, South Africa. Long term rainfall records are available for the Hluhluwe research station, where average annual rainfall from 1985 to 2006 was 960mm. The wet season (monthly rainfall ~120-140mm) spans the summer months from October to February; rainfall is weakly bimodal with maximum rain falling in November and in February (see Figure 5.1). The dry season (monthly rainfall ~20-60mm) spans the winter months from March to September. Monthly rainfall of less than 60mm to 80mm in some months is considered sufficiently seasonal for tree ring formation.

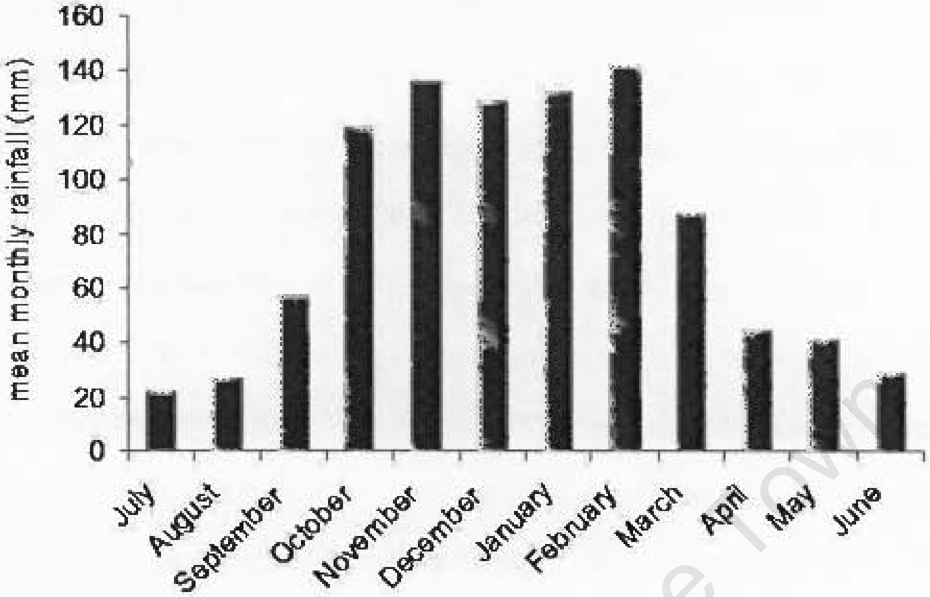

Figure 5.1. Mean monthly rainfall from 1985 to 2006.

We included the three most common and widespread *Acacia* species in the area. Saplings of *A. karroo* are particularly common especially in the mesic northern part of the park, and it is an important bush encroaching species in southern Africa. *A. nilotica* and *A. nigrescens* are both common as adults, *A. nilotica* in the mesic north and center and *A. nigrescens* in the semi-arid south, but recruitment of both species appears to have decreased dramatically. A method for age determination by ring counts would contribute to ecological studies of each of these species.

Discs were cut from five trees of each species at between 0.5m and 1.5m from the ground. We sampled five *A. karroo* trees, three each *A. nilotica*, and three *A. nigrescens* trees. We also included two *A. nilotica* trees and two *A. nigrescens* trees sampled in 2003 in the same park by February *et al.* (2006). Because sampling is destructive, trees were selected that had been fatally damaged by elephants.

Discs were prepared for microscopy by polishing using progressively finer sandpaper on a belt sander (4" Makita, Japan) after February *et al.* (2006). They were then scanned at 3600 dpi (HP ScanJet 3970 Series) and the images imported into Cybis CooRecorder (Larsson 2006). This program was used for recording bands of marginal parenchyma (see Gourlay & Kanowski 1991; Gourlay & Grime 1994; Wyant & Reid 1994; Gourlay 1995) along two radii after they were traced around the entire disc under a Wild M3C (Wild, Heerbrugg, Switzerland) stereoscopic microscope, at between 15x and 50x magnification. Tree rings from each study species are shown in Figure 5.2.

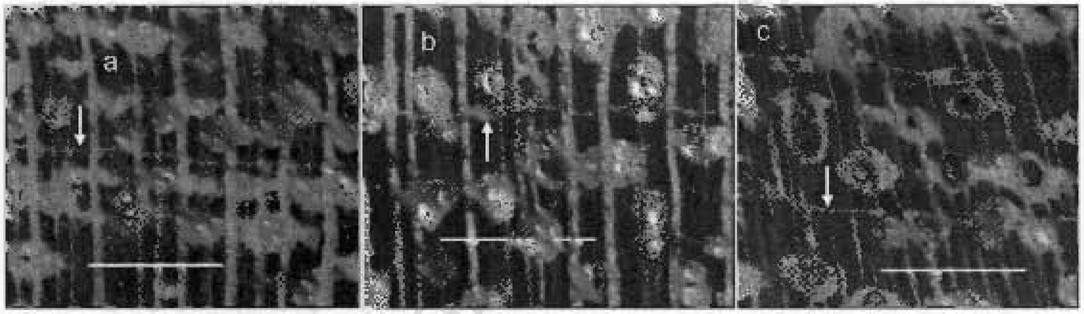

Figure 5.2. Pictures of rings in a) *Acacia karroo*, b) *A. nilotica*, and c) *A. nigrescens*. Arrows indicate rings formed by bands of marginal parenchyma that form the boundary of approx. one year of growth. Scale bars of 1mm included.

Samples for radiocarbon dating were extracted with an electric drill (Metabo, Germany) from the center of each disc using a 1.5mm diameter drill bit. The resulting sawdust was collected and sent to the Center for Applied Isotope Studies at the University of Georgia for AMS radiocarbon dating. Dates were calibrated by the lab using the method outlined in Hua and Barbetti (2004).

Results

We encountered similar challenges with tree ring identification as other authors (see Martin & Moss 1997), mostly because marginal parenchyma are microscopic features in *Acacia* wood (see Figure 5.2) and can be difficult to identify among other, larger wood features. However, rings are consistently identifiable, especially when an entire tree cross section is available on which rings can be traced.

Table 5.1. Details of samples from *Acacia* species used in this study.

	^{14}C sample	ring count	^{14}C age		mean ring width (mm)	mean growth (mm / yr)
A. karroo						
Akar1	01866	25	17		1.55	2.29
Akar2	01870	11	10		2.37	2.61
Akar3	01871	8	10		4.15	3.32
Akar4	01872	17	12		1.63	2.31
Akar5	01873	14	12		1.47	1.72
				Mean	2.44	2.24
				St dev	0.59	1.13
A. nilotica						
Anil1	09121	12	19		see February *et al.* 2006	
Anil2	09123	19	27		see February *et al.* 2006	
Anil3	01867	27	33		3.00	2.46
Anil4	01868	38	49		3.37	2.62
Anil5	01869	46	48		1.85	1.78
				Mean	1.86	2.34
				St dev	0.92	1.03
A. nigrescens						
Anig1	09122	34	45		see February *et al.* 2006	
Anig2	09126	39	35		see February *et al.* 2006	
Anig3	02264/65	103	88		1.89	2.63
Anig4	02266	23	28		1.15	0.94
Anig5	02267	43	38		2.53	2.86
				Mean	1.86	2.14
				St dev	0.69	1.05

Details of samples of *Acacia* species used in this study are listed in Table 5.1 with ring counts and ^{14}C ages. Tree ring counts consistently underestimate true age for the *Acacia* species used for this study, but relationships of ring count to age are strong (see Figure 5.3 and Table 5.2). *A. karroo* forms 2.38 rings per year (r^2=0.930, p=0.0081), with a standard error for age estimates of ±0.87 years and a y-intercept of 5.85 years. *A. nilotica* forms 1.09 rings per year ($r^2=0.941$, $p=0.0062$), with a standard error for age estimates of ±3.58 years and a y-intercept of 8.78 years. *A. nigrescens* forms 1.39 rings per year ($r^2=0.952$, $p=0.0045$), with a standard error for age estimates of ±5.20 years and a y-intercept of 14.10 years. All relationships are characterized by an intercept of 5 to 15 years and by slightly more than one or slightly more than two rings per year.

Table 5.2. Statistics and regression equations for the relationship between ^{14}C age and ring count. See also Figure 5.3 (below).

	R^2	p	fit equation	std error (years)	rings / year (1/slope)	false ring freq (yrs)
A. karroo	0.930	0.0081	age 5.85+0.42*rings	±0.87	2.38	2.63
A. nilotica	0.941	0.0062	age 8.78+0.92*rings	±3.58	1.09	11.1
A. nigrescens	0.952	0.0045	age 14.10−0.72*rings	±5.20	1.39	2.52

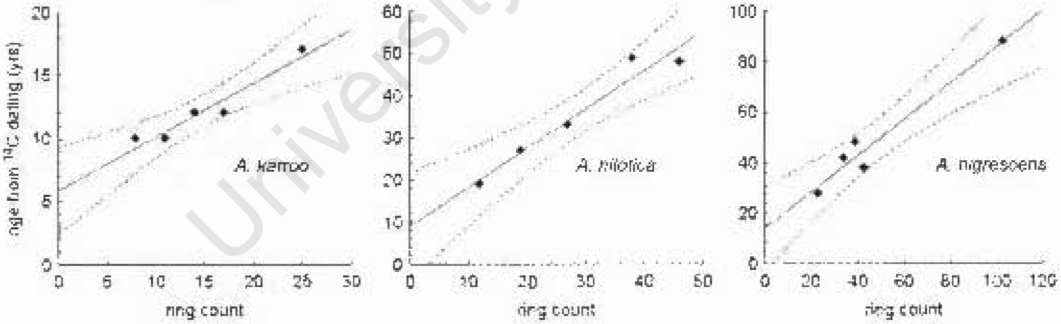

Figure 5.3. Ring count versus age. Bands represent 95% confidence intervals. See Table 5.2 (above) for statistics and regression equations for all species.

Neither tree height nor tree radius was a good predictor of tree age. For five *A. karroo* trees, tree height was not related to age ($r^2=0.121$, $p=0.57$) and tree radius was not related to age ($r^2=0.336$, $p=0.306$). Unfortunately, we were only able to include three individuals each of *A. nilotica* and *A. nigrescens* and could not include trees dated by February *et al.* (2006) because they did not report height and radius for the trees they sampled. We were unable to establish relationships between tree height and age and tree radius and age.

A. karroo grew from 1.72mm to 3.32mm per year with mean annual growth of 2.24mm and a standard deviation of 1.13mm (see Table 5.1). *A. nilotica* grew from 1.78mm to 2.62mm per year with mean annual growth of 2.34mm and a standard deviation of 1.03mm. *A. nigrescens* grew from 0.94mm to 2.86mm per year with mean annual growth of 2.14mm and a standard deviation of 1.05mm. Data on growth rates of African *Acacia* species are scarce, but these ring widths are substantially smaller than those demonstrated by Gourlay (1995) in East Africa by a similar method (6.3mm to 19.18mm per ring). Prins and van der Jeugd (1993) also document higher growth rates in East Africa than those observed in this study as well (4.3mm to 6.4mm per year).

Discussion

Relationships between ring counts and true age of the species of *Acacia* considered here are strong. Ring counts can be used to predict true age to a fair degree of accuracy (approx. ±1 year for *A. karroo*, ±4 years for *A. nilotica*, ±5 for *A. nigrescens*). However, species-specific calibrations of ring count-true age relationships, possibly via radiocarbon dating, are clearly necessary.

Species included in this study have different age – ring count relationships. *A. karroo* forms approximately two rings per growing season, while *A. nilotica* and *A. nigrescens* form only one, even though *A. karroo* and *A. nilotica* have overlapping distributions. Because ring formation in *Acacia* trees is closely associated with changes in water availability (Gourlay 1995), this indicates that *A. karroo* may be more sensitive to the small mid-wet season dip in rainfall than *A. nilotica*. Moreover, *A. karroo* appears to form more 'false rings' (2.38 rings per year is an extra ring every 3 years) than *A. nilotica* (1.09 rings per year is an extra ring every 11 years). This also suggests that growth or at least ring formation in *A. karroo* is more sensitive to intra-annual variation in rainfall than in *A. nilotica*. *A. nigrescens* occurs in more arid areas than both *A. nilotica* and *A. karroo*, which may explain why it forms more 'false rings' (1.39 rings per year is an extra ring every 3 years) than *A. nilotica*. Unfortunately, information on rainfall sensitivity of *Acacia* species with which to compare this data is not readily available.

We chose not to force y-intercepts through zero for relationships between radiocarbon dates and ring counts (see Figure 5.3), and y-intercepts are substantial (5.85 years for *A. karroo*, 8.78 years for *A. nilotica*, and 14.1 years for *A. nigrescens*). If the stems sampled for this study established as new seedlings, they may have been more sensitive to water stress or may have been sourcing water from shallower soil horizons than adults (Weltzin & McPherson 1997), where soil moisture is more variable. Alternatively, the sampled stems may have resprouted from established roots of saplings damaged by herbivory or fire. These root systems can be extensive (pers. obs.) and would enable small shoots to source water from similar soil horizons to adults (Weltzin & McPherson 1997). In this case, resprouting from stored starch reserves (Miyanishi & Kellman 1986; Canadell & López-Soria 1998) could result in tree ring formation that is not related to annual rainfall seasonality.

Clarifying the physiological and climatic causes of ring formation in *Acacia* species, particularly at younger life stages will be a vital step for validating the use of rings of marginal parenchyma to age these savanna trees. Gourlay (1995) has linked the formation of these bands to changes in moisture availability. The bands are often filled with chains of calcium oxalate crystals, depending on the aridity of the site and on mineral composition of soils. However, much work remains to pin down the physiology of ring formation, which is well established for the temperate forest trees used for traditional dendrochronology (Fritts 1976; Schweingruber 1996). The cambial injury approach used by Wyant and Reid (1992) might contribute.

Tree ring counts using marginal parenchyma bands in *A. karroo*, *A. nilotica*, and *A. nigrescens* provide a good way to estimate age of trees. Radiocarbon dating, as in this study, or some other method of assessing true age is necessary to calibrate robust relationships between age and ring counts.

Chapter 6

Continuous versus episodic recruitment in three African *Acacia* species

A. Carla Staver, William J. Bond & Edmund C. February

Introduction

Savanna is defined by having a continuous grass layer and a discontinuous tree layer and is among the most globally widespread biomes (Skarpe 1992; Scholes & Archer 1997). Savannas occur in diverse areas of high and low rainfall and of variable soil fertility, making them difficult to define on the basis of climatic and edaphic features alone. Since the beginning of the last century, the dominant paradigm for explaining tree grass coexistence – the Walter hypothesis – suggested that trees and grasses do not actually compete because trees source water from deeper soil horizons and grasses source more ephemeral water from shallower soil horizons, resulting in potentially stable tree-grass coexistence (Walter 1971; Walker & Noy-Meir 1982). This equilibrium approach to savannas has been seriously criticized (Ellis & Swift 1988; Westoby *et al.* 1989; Sullivan & Rohde 2002; Briske *et al.* 2003). Savannas can vary much more widely than equilibrium concepts allow, even over relatively short time periods (Walker *et al.* 1981; Westoby *et al.* 1989; Gillson 2004) and are often not at equilibrium with long term climate averages (Bond 2005; Bond *et al.* 2005; Sankaran *et al.* 2005).

Rainfall, fire and herbivory are widely considered to be among the major determinants of savanna structure (Scholes & Archer 1997). Although rainfall is often assumed to be stable – mean annual rainfall is often used in assessing distribution of savanna relative to rainfall (Scholes & Walker 1993; Bond *et al.* 2005; Sankaran *et al.* 2005) – variability in rainfall may be important in determining the way that trees establish in savannas, thereby shaping savanna structure. In arid savannas, seedling establishment may happen primarily in years with exceptionally high rainfall (O'Connor 1995; Watson *et al.* 1997; Wiegand *et al.* 1999; Wiegand *et al.* 2004), resulting in even aged tree cohorts; the extent to which episodic seedling establishment shapes tree population dynamics is unknown, however, and seedling establishment often does not dominate tree population dynamics (Watson *et al.* 1997; Brown & Archer 1999; Wiegand *et al.* 1999; Wiegand *et al.* 2004). In mesic and semi-arid savannas, interannual rainfall variability determines grass growth, fuel loads, and fire intensity (Scholes & Archer 1997; Higgins *et al.* 2000; Balfour & Howison 2001; Knapp *et al.* 2001) and potentially influences tree growth directly (Miller *et al.* 2001).

Fire and browsing can suppress tree cover below its climate potential (Prins & van der Jeugd 1993; Bond *et al.* 2005; Sankaran *et al.* 2005), while grazing decreases standing grass biomass, resulting in decreases in the effects of grass competition and fire on tree cover (Walker & Noy-Meir 1982; Madany & West 1983; Sharp & Whittaker 2003; van Langevelde *et al.* 2003; Archibald *et al.* 2005; Collins & Smith 2006). Fire, browsing, and grazing are highly variable both spatially and temporally. This variability may be fundamental to the dynamics and demography of savanna trees.

Fire is an event, and therefore necessarily temporally variable. Higgins *et al.* (2000) suggest a mechanism for this discontinuous disturbance to regulate tree cover. They argue that fire limits tree cover by preventing the recruitment of tree saplings into adults (see also Hoffmann 1999) rather than by killing existing adult trees (Williams *et al.* 1999). Savanna saplings survive fire by resprouting after shoots are burnt (Miyanishi & Kellman 1986; Hoffmann 1998) until they manage to escape the 'fire trap' between fires by growing into adult trees (Higgins *et al.* 2000; Gardner 2006). Variation in fire interval is important to the biological response of trees to fire; frequent fires suppress saplings, which recruit into adults only when time between fires is long enough (Higgins *et al.*

2000). Fire is also an inherently spatial process (Urban *et al.* 1987; Heyerdahl *et al.* 2001), introducing more heterogeneity into savannas (Eckhardt *et al.* 2000; Moreira 2000; van Wilgen *et al.* 2003; D'Odorico *et al.* 2006) in patches at multiple scales (Baker 1993).

The role of herbivory in influencing tree cover in savannas is more difficult to generalize, in part because the impacts of mammal herbivory depend on whether grazing or browsing predominates. Intense grazing pressure has often been linked to increases in woody cover (Archer 1990; Roques *et al.* 2001; Sharp & Whittaker 2003), due to decreases in fire intensity (Sharp & Whittaker 2003; van Langevelde *et al.* 2003; Archibald *et al.* 2005; Collins & Smith 2006), decreases in grass competition (Walter 1971; Walker & Noy-Meir 1982; Madany & West 1983), and even increased dispersal (Brown & Archer 1999). Herbivore pressure often varies substantially across a landscape (Coughenour 1991; Bailey *et al.* 1996; Schwinning & Parsons 1999). Where both browsing and grazing are important in the landscape, especially in areas with extant native herbivore assemblages, herbivory more often results in suppression of tree recruitment. Browsing by mesoherbivores, particularly impala, suppresses sapling growth (see Chapter 4 in this volume; Belsky 1984; Barnes 2001; Augustine & McNaughton 2004; Sharam *et al.* 2006), preventing recruitment of saplings into adults (Prins & van der Jeugd 1993; Barnes 2001). As with fire, a temporary reduction in herbivore use intensity can result in recruitment of saplings into adults; temporal variability in herbivory may be a key factor in savanna tree dynamics (Prins & van der Jeugd 1993). Both browsing and grazing are spatially and temporally variable

(Coughenour 1991; Young 1994; Bailey *et al.* 1996; Schwinning & Parsons 1999; Redfern *et al.* 2005), introducing heterogeneity into savanna ecosystems (du Toit 2003).

Spatial and temporal variation are scale-dependent. Scale of observation often determines what types of variation are observed and what types of drivers are perceived as responsible for variation (Coughenour & Ellis 1993; Gillson 2004). Gillson (2004) used long term pollen records to demonstrate hierarchical patch dynamics; high levels of variability at local scales aggregate, resulting in stability at a regional scale constrained by climate. In fact, climatic drivers are often discussed as primary determinants of savanna structure at regional and continental scales (Williams *et al.* 1996; Scholes *et al.* 2002), while fire and herbivory are usually discussed more locally (Eckhardt *et al.* 2000; Moreira 2000; du Toit 2003; van Wilgen *et al.* 2003; D'Odorico *et al.* 2006). Explicit considerations of spatial and temporal variability at multiple scales are clearly vital in discussions of what processes structure savannas.

The above discussion suggests two major points: 1) woody cover is suppressed by fire and herbivory preventing demographic transition of saplings to adult trees, and 2) rainfall, fire, and herbivory are temporally and spatially variable features at multiple scales whose effects on savannas are probably explicitly temporal and spatial. We present here the results of a study examining the temporally and spatially variable establishment of adult *Acacia* trees. We wished to establish whether tree recruitment was continuous, consistent with 'equilibrium' savanna models, and if not, whether variable recruitment was related to special conditions or events identifiable from rainfall, herbivore population, or fire records for the park. Trees of each of three species of *Acacia* were sampled from different patch sizes and aged using dendrochronology techniques (see Chapter 5 in this volume; Gourlay & Grime 1994; Gourlay 1995) to establish population structure. The ageing method essentially establishes ages for successful stems; if an individual resprouted from the base after a fire, for instance, we aged the stem that became an adult, rather than the time of establishment of the individual. Thus, results reflected sapling release events rather than seedling establishment events. The approach was explicitly demographic, and spatial structuring of samples at multiple scales allowed us to ask whether population structure differed depending on scale. By contrasting tree ages with rainfall, fire and herbivory records, we inferred what drivers were responsible for sapling release.

Study Area

The study was conducted in Hluhluwe iMfolozi Park (900 km^2; 28°00' – 28°26' S; 31°43' – 32°09' E), located in northern KwaZulu Natal, South Africa. Topography is varied, consisting mainly of rolling hills of up to 540m elevation in the Hluhluwe Game Reserve area falling into broader river valleys at 40m elevation in the iMfolozi Game Reserve area. Soil types are closely linked to bedrock geology (Graham 1992), consisting predominantly of shales and sandstones with intermittent doleritic intrusions (King 1970; Graham 1992). Because slopes are steep, catenary sequences that dominate soils in other African savannas are not distinct in this area.

Rainfall is closely linked to elevation within the park (Balfour & Howison 2001), producing a rainfall gradient between higher elevation Hluhluwe GR and lower elevation iMfolozi GR. The longest rainfall series comes from Hilltop Tourist Camp in Hluhluwe, where rainfall in the park is highest, and spans 1933 to 2006. Average annual rainfall was 974mm. A maximum rainfall of 1594mm fell during the 1957/1958 season and a minimum of 517mm during the 1991/1992 season. Hluhluwe daily temperatures range between ~39°C (mean daily T_{max}) and ~15°C (mean daily T_{min}) in summer and between ~32°C and ~9°C in winter. iMfolozi daily temperatures range between ~40°C and ~14°C in summer and between ~34°C and ~6°C in winter (Zululand Tree Project baseline data).

The two reserves constitute ecologically distinct areas characterized by different plant species composition and fire frequency and large mammal herbivore pressure. Most areas in the Hluhluwe Reserve, including areas of relatively low rainfall, have burned more than 10 times between 1956 and 1996, while most areas in the iMfolozi Reserve have burned only between one and eight times during the same period (Balfour & Howison 2001). Large mammal herbivore densities within and between reserves vary depending on herbivore habitat preferences. Impala (*Aepyceros melampus*) are by far the most numerous herbivore in the park and occur with higher densities in semi-arid iMfolozi (36 per km^2) than in mesic Hluhluwe (24 per km^2); white rhino (*Ceratotherium simum*) make up the largest biomass in the park with higher densities in iMfolozi (2.5 per km^2) than Hluhluwe (1.8 per km^2). Herbivore densities have fluctuated substantially during the past century in Hluhluwe iMfolozi Park, largely due to hunting, the rinderpest epidemic, and culling campaigns during the early part of the 20th century associated with efforts to eradicate the *nagana* livestock disease. However, herbivore densities have recuperated and have been dramatically higher during the last 20 years than at any point during the preceding century. The park currently employs drought mitigation strategies, including limiting fire during dry periods and controlling animal populations, to minimize widespread death of game from drought.

Methods

A total of 125 adult trees each of *Acacia karroo*, *A. nilotica*, and *A. nigrescens* were sampled for ring counts. Samples were structured spatially to determine not only if recruitment is event-driven but also to give an approximation of the scale of event that drives recruitment. Within the park landscape, five areas of 0.25 km^2 (25 ha) were randomly selected to represent a 'hillside' and 25 trees sampled in each. Within each hillside, five stands of trees were randomly selected and five trees sampled within an area of 0.25 ha. Thus, spatially structured sampling with five hillsides of five stands each of five trees each makes up a sample of 125 trees total, which represent the whole park, or landscape. Figure 6.1 shows a schematic of sampling stratification at multiple scales, as well as locations of hillsides in Hluhluwe iMfolozi Park. Note that trees, stands, and hillsides were sampled randomly as long as there were sufficient trees in an area to fit a plot and at a distance of not closer than two kilometers from the next closest hillside sampled or 100m from the next closest stand sampled. Discs were cut from each tree at between 0.5m and 1.5m from the ground. Because sampling is destructive, trees were selected that had been fatally damaged by elephants.

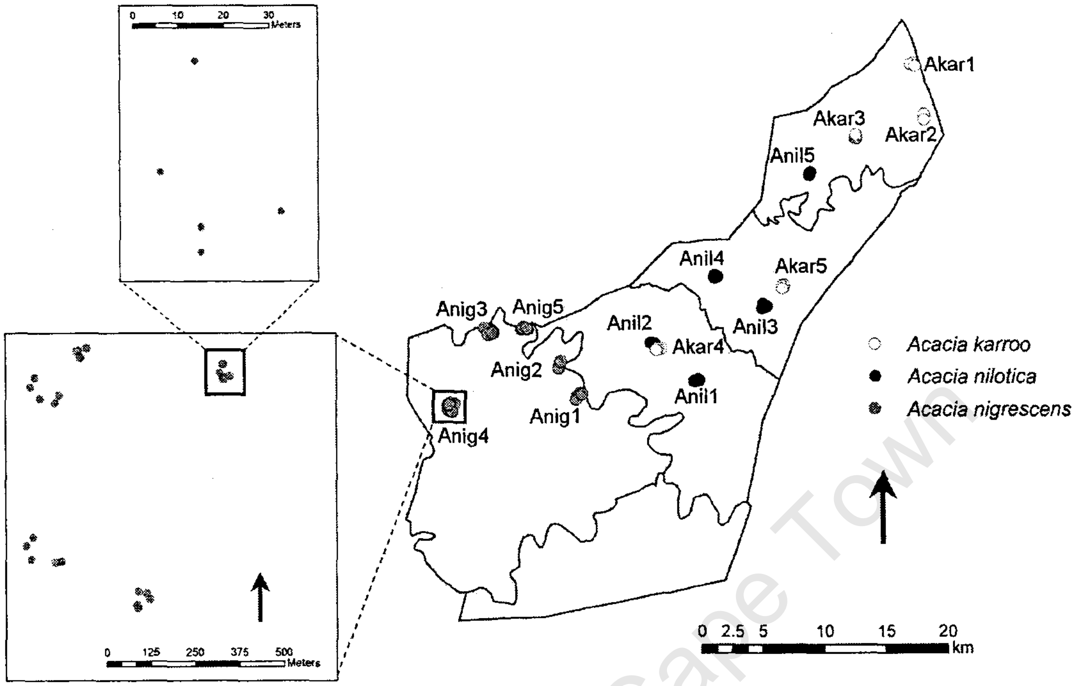

Figure 6.1. Sampling locations in Hluhluwe iMfolozi Park. Sampling was structured spatially into the five 'hillsides', each of 2.5 ha, located within a 'landscape'. Five stands of five trees each were sampled on each hillside, resulting in a total sample of 125 trees of each of three species ('Akar' = *Acacia karroo*; 'Anil' = *A. nilotica*; 'Anig' = *A. nigrescens*).

Discs were prepared for microscopy by polishing using progressively finer sandpaper on a belt sander (4" Makita, Japan) after February *et al.* (2006). They were then scanned at 3600 dpi (HP ScanJet 3970 Series) and the images imported into Cybis CooRecorder (Larsson 2006). This program was used for recording bands of marginal parenchyma (see Gourlay & Grime 1994; Gourlay 1995) along two radii after they were traced around the entire disc under a Wild M3C (Wild, Heerbrugg, Switzerland) stereoscopic microscope, at between 15x and 50x magnification. Ring counts were calibrated to tree age via radiocarbon dating of a sub-sample of 5 trees for each species that span the range of tree ring counts found in this study (see Chapter 5). Ring counts provide reliable estimates for ^{14}C age to ±0.87 years for *A. karroo*, to ±3.58 for *A. nilotica*, and to ±5.20 for *A. nigrescens.*

History of *Acacia* recruitment, derived from ring counts, was first evaluated for spatiotemporal structure in recruitment at landscape, hillside, and stand scales separately. Recruitment was considered to occur in 'episodes' when recruitment occurred for fewer than 5 years and in extended periods when recruitment occurred for more than 10 years.

Timing of recruitment was then compared to long-term records of rainfall, fire, and herbivore populations. Complete rainfall records are available from the research station in Hluhluwe from 1933. This record was used for relating *A. karroo* and *A. nilotica* recruitment to rainfall but is too recent for comparison with *A. nigrescens* recruitment. Complete rainfall records are available from the Durban Botanical Gardens through the South African Weather Service starting in 1871. Annual rainfall in Durban is broadly related to annual rainfall in Hluhluwe between 1933 and 2005 (r^2=0.397, p<0.0001). Fire maps are available for the park from 1955, from which fire histories of each plot were extracted. Records of fires before 1955 are anecdotal; fires were set at the northern end of the park where *A. karroo* and *A. nilotica* occur and suppressed at the southern end where *A. nigrescens* occurs. Herbivore population estimates were done consistently every year from 1978, and less regular estimates are available from 1929 in Hluhluwe and 1952 in iMfolozi. Herbivore numbers are impossible to estimate reliably from anecdotal accounts from before this time.

Fire records were compared to recruitment at landscape, hillside, and stand scales, because records were spatially explicit; however, rainfall and herbivore populations were only compared to recruitment at the landscape scale, because historical records are not spatially explicit and are only valid for the entire park.

Results

The three *Acacia* species selected for this study yielded clear and countable tree rings that provided estimates of tree age. The oldest adult *A. karroo* established in 1989 and was 17 years old, the oldest *A. nilotica* in 1946 and was 60 years old, and the oldest *A. nigrescens* in 1909 and was 98 years old. *A. karroo* trees begin to senesce at around 30 years of age (Gourlay *et al.* 1996); these trees had not reached maximum age for the species. Independent maximum age estimates were not available for *A. nilotica* and *A. nigrescens*. *A. erioloba*, a species found in arid savannas in Southern Africa is known to reach up to 300 years old (Timberlake 1980). *Burkea africana*, another common African savanna tree species, has documented ages of 115 years (Wilson & Witkowski 2003). Maximum ages for *A. nilotica* and *A. nigrescens* found in this study were within a reasonable range for savanna trees in general; maximum age of *A. karroo* was young compared to expected ages for that species.

RECRUITMENT OF *Acacia karroo*

Recruitment of most of the adult *A. karroo* present in the landscape began around 1992, continued for four years until 1996, and declined (see Figure 6.2). This period of recruitment was concurrent with a period of drought, high herbivore densities, and very little fire. Although isolating the effects of any of these factors is impossible, decreases in rainfall and related changes in disturbances from herbivory and fire clearly had a major impact on recruitment rates of *A. karroo*.

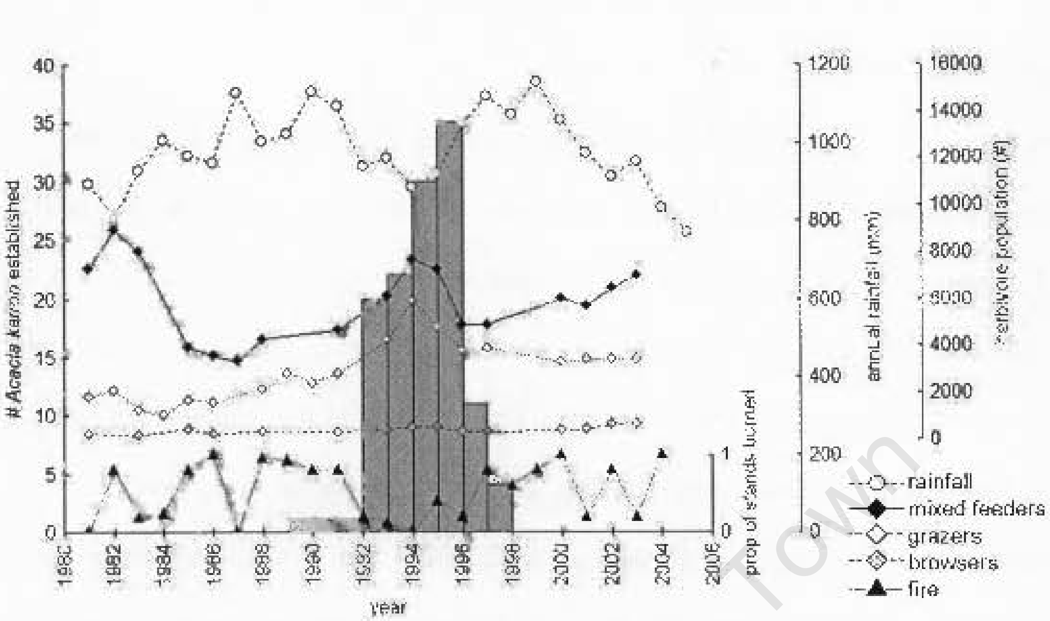

Figure 6.2. Timing of recruitment of adult *A. karroo* in Hluhluwe iMfolozi Park. *A. karroo* adults now present in the landscape began recruiting in 1992, concurrent with a relatively dry period with little fire and an increase in grazer and mixed feeder densities. Recruitment dropped off around 1996, at the end of this period.

Because of differences in variance among populations and non-normal distributions (see Figure 6.3), a non-parametric Kruskal-Wallis ANOVA was used to determine whether the timing of recruitment differed among hillsides. Recruitment occurred at different times and with different intensities depending on location within the landscape (H=33.7, p<0.0001). Comparison with local fire histories revealed that on three hillsides (Akar1, Akar4, Akar5), recruitment of adult *A. karroo* occurred during extended periods (~four years) with no fire (see Figure 6.3). The two remaining hillsides did not have extended periods without fire, but recruitment occurred during period with less frequent fire. Recruitment of *A. karroo* is related to decreases in fire frequency and especially periods of no fire at the local, hillside scale.

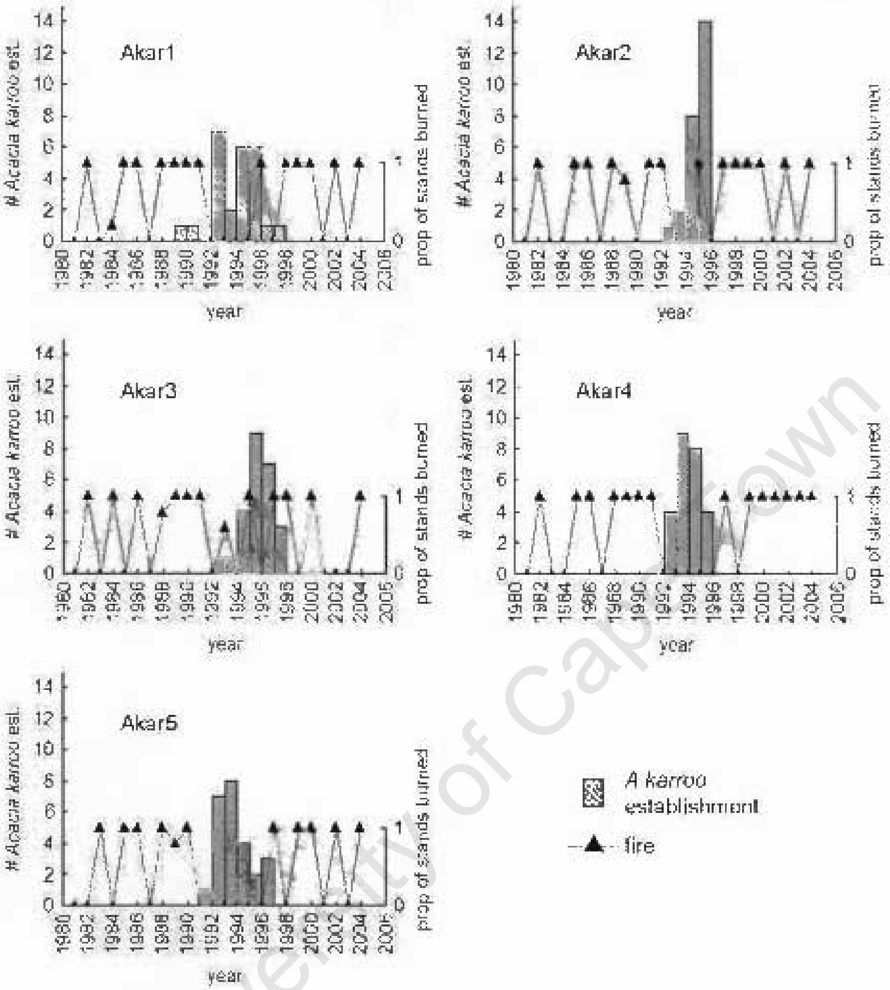

Figure 6.3. Timing of recruitment of adult *A. karroo* on five hillsides in Hluhluwe iMfolozi Park. On three hillsides (Akar1, Akar4, Akar5), recruitment of *A. karroo* adults now present was concurrent with period of no fire of approximately four years. Differences in ages of *A. karroo* adults on these hillsides were significant (K-W ANOVA: H=33.7; p<0.0001).

Ages of adult *A. karroo* also differed significantly among stands (H=70.4, p<0.0001) (see Figure 6.4). Some hillsides had even-aged stands across the entire hillside (Akar2, Akar4) or had trees with more variable age across the entire hillside (Akar1). However, others hillsides had substantial variation among stands within the hillside (Akar 3, Akar5). Recruitment on 'Akar3', in particular, was not characterized by an extended period of no fire; fire may have acted on a smaller, stand scale to limit recruitment and then permit release of adult *A. karroo* on this hillside. However, fire records are not spatially detailed enough to allow such fine-scale comparison.

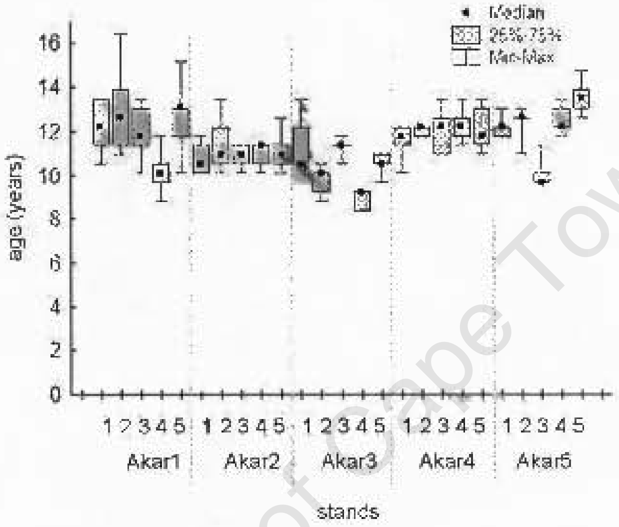

Figure 6.4. Ages of *A. karroo* adults in Hluhluwe iMfolozi Park. Medians, quartiles and ranges are presented for each stand of live trees. Five stands were sampled from each of five hillsides in the park. Hillside three (Akar3) demonstrated recruitment events sometimes occurred in stand-sized patches. Differences in ages of *A. karroo* adults among stands were significant (K-W ANOVA: H=70.4; p<0.0001).

Recruitment of *A. karroo* is discontinuous and related to rainfall variability, herbivore densities, and fire at a landscape scale. It is variable at local/hillside and stand scales as well, suggesting that spatial variation in fire, and possibly in herbivore densities, are key determinants that limit establishment of adult *A. karroo*.

RECRUITMENT OF *Acacia nilotica*

Recruitment of most of the *A. nilotica* present in the landscape began around 1957 and increased until 1965, dropped off drastically for three years, began again in 1970, and continued until 1975 (see Figure 6.5). Low levels of recruitment of adults continued until 1985. Recruitment was undoubtedly discontinuous at the landscape scale, but recruitment episodes (<5 yrs long) were probably less important than extended periods (more than 10 years) of recruitment punctuated by periods of no recruitment.

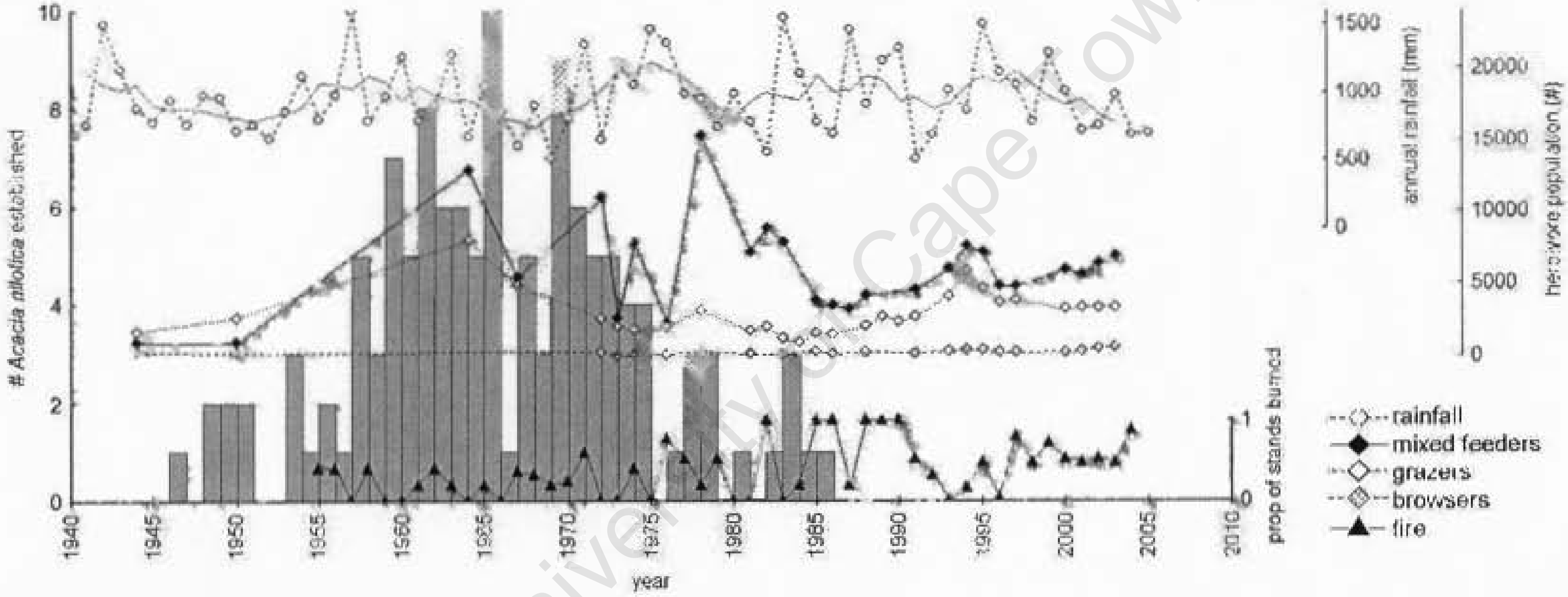

Figure 6.5. Timing of recruitment of adult *A. nilotica* in Hluhluwe iMfolozi Park. Recruitment of *A. nilotica* adults was discontinuous, with long periods with more frequent recruitment. Recruitment of most *A. nilotica* adults currently present in the landscape began around 1953 and continued until 1975 with a substantial lull in recruitment in 1967 to 1969. Relationships to annual rainfall, herbivore densities, and fire were unclear on the landscape scale.

No relationship between *A. nilotica* recruitment and variations in rainfall, herbivore densities, and fire was evident. There was an increase in fire frequency and extent in about 1980, when recruitment declined drastically, but because fire records extend only to 1955, a similar comparison to the time when recruitment began is impossible. There was no marked increase in the proportion of stands burning during the lull in recruitment from 1967 to 1969.

Again, a non-parametric Kruskal-Wallis ANOVA was used to determine whether the timing of recruitment differed among hillsides because of unequal variance among hillsides and non-normal distributions (see Figure 6.6). Recruitment occurred at different times and with different intensities depending on location within the landscape (H=38.9, p<0.0001). Comparisons with local fire histories shows that on three hillsides (Anil1, Anil2, Anil3), recruitment of *A. nilotica* adults occurred during periods of low fire frequency. On another (Anil4) recruitment occurred earlier during a period of moderate fire frequency and was followed by a period of low fire frequency; seedlings or saplings of *A. nilotica* that were present in the area might have already escaped and recruited into adults by the time fire frequency decreased. On another hillside (Anil5), however, recruitment occurred well after an extended period without fire. Timing of recruitment of the *A. nilotica* adults present certainly varied among hillsides in the landscape, but conclusively linking variations to changes in fire frequency was impossible. Decreases in fire frequency may have played a role in allowing *A. nilotica* adults to establish. Unfortunately, long-term local herbivore density estimates were not available.

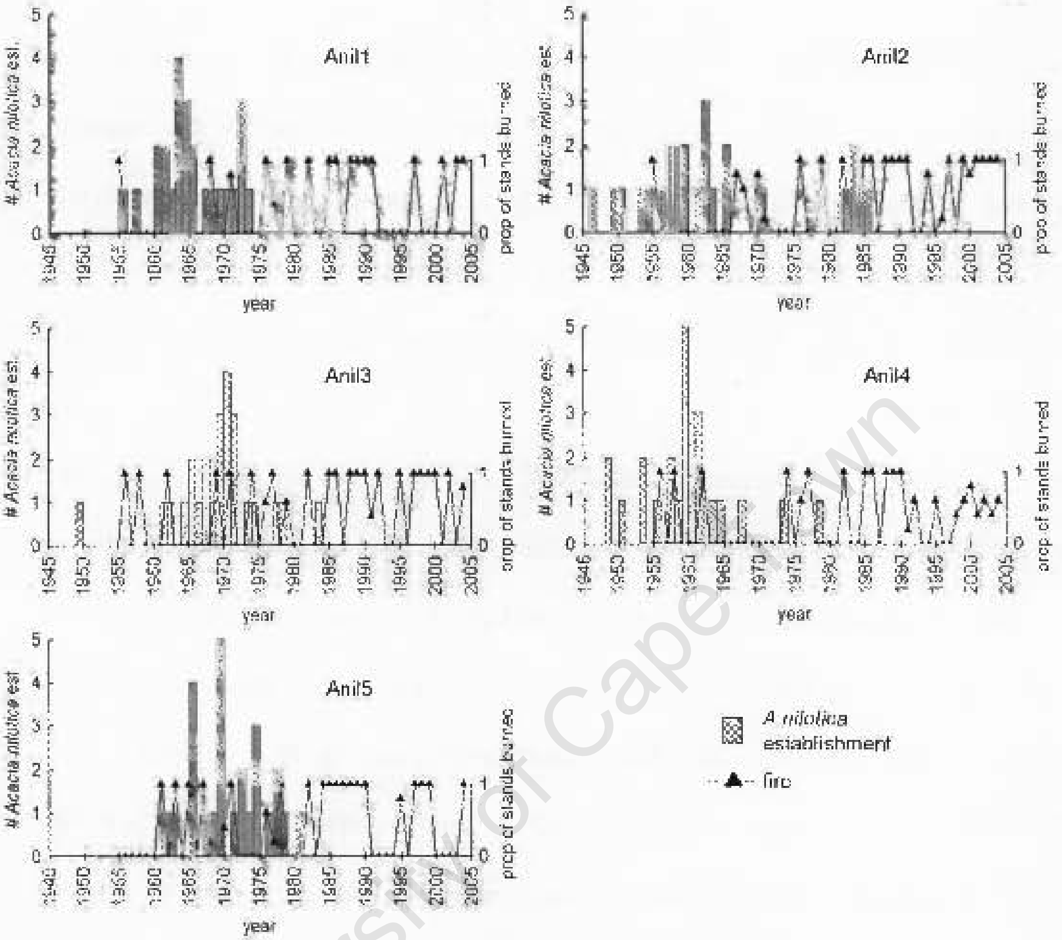

Figure 6.6. Timing of recruitment of adult *A. nilotica* on five hillsides in Hluhluwe iMfolozi Park. On three hillsides (Anil1, Anil2, Anil3), recruitment of *A. nilotica* adults now present was concurrent with periods of relatively low fire frequency. Differences in ages of *A. nilotica* adults on these hillsides were significant (K-W ANOVA: H=38.9; p<0.0001).

Ages of adult *A. nilotica* also differed significantly among stands (H=77.8, p<0.0001) (see Figure 6.7). For the most part, tree age was variable across entire hillsides (Anil1, Anil3, Anil4). However, one hillside (Anil2) had one stand of a clearly different cohort than the rest. Another (Anil5) showed significant differentiation in age among stands. These stands showed that even-aged cohorts resulting from an episode at a small scale certainly did occur and probably contributed to the observed population structure of *A. nilotica*. Small-scale episodes may have been widespread in the landscape, but were impossible to detect by this method where these cohorts were not spatially separated into distinct patches.

Recruitment of *A. nilotica* is discontinuous at a landscape scale, but did not appear to be strongly related to rainfall variability, herbivore densities, or fire history. It is variable at local/hillside and stand scales as well, suggesting that spatial variability in recruitment played a role in *A. nilotica* population dynamics. At large scales, discontinuity in recruitment was characterized by longer term periods of recruitment rather than by recruitment episodes. However, cohorts of trees of the same age emerged at finer scales. Long term periods of recruitment at larger scales may have resulted from coalescing cohorts and clumps at finer temporal and spatial scales. Following a rather extended period of recruitment, very few *A. nilotica* have become adults since 1985; this suggests that recruitment of *A. nilotica* adults has stopped.

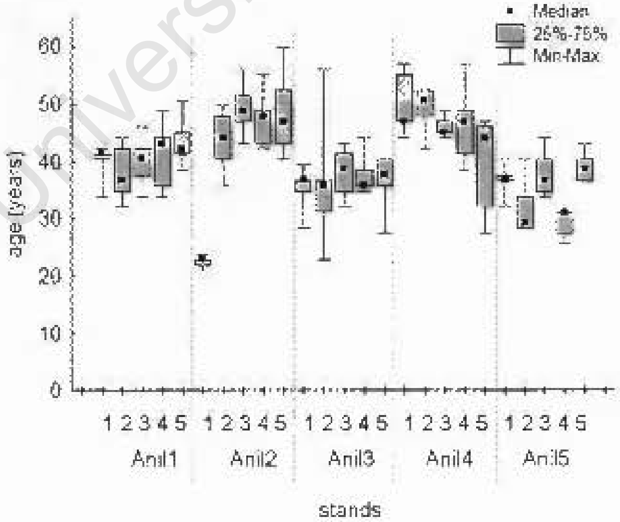

Figure 6.7. Ages of *A. nilotica* adults in Hluhluwe iMfolozi Park. Medians, quartiles and ranges are presented for each stand of five trees. Five stands were sampled from each of five hillsides in the park. Stand one in hillside two (Anil2.1) and hillside five (Anil5) demonstrated that recruitment of *A. nilotica* sometimes occurred in stand-sized patches. Differences in ages of adults in these stands are significant (K-W ANOVA: H=77.8; p<0.0001).

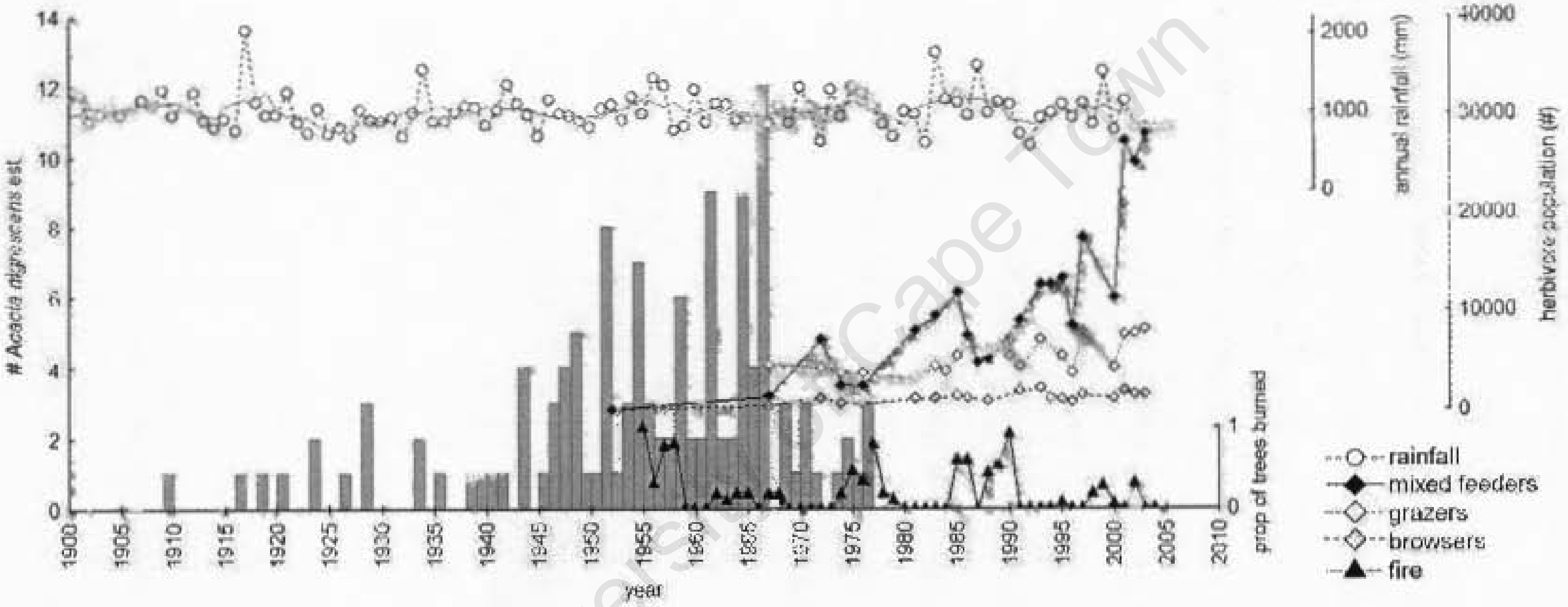

Figure 6.8. Timing of recruitment of adult *A. nigrescens* in Hluhluwe iMfolozi Park. Recruitment of *A. nigrescens* adults was discontinuous, with more frequent recruitment in some years than in others. No young adults of *A. nigrescens* were found, indicating that recruitment stopped around 1977. Although fire and herbivore density records were too recent for comparison, the decline in recruitment of *A. nigrescens* was concurrent with dramatic increases in herbivore densities, particularly of mixed feeders, and with an end to fire suppression in parts of iMfolozi GR.

RECRUITMENT OF *Acacia nigrescens*

Recruitment of most of the *A. nigrescens* present in the landscape occurred between 1943 and 1977 (see Figure 6.8). However, rates of recruitment of adults were variable from year to year during this time; particularly high recruitment occurred in 1951, 1954, 1958, 1961, 1964, and 1966. No young adults of *A nigrescens* were found, indicating that recruitment stopped in the entire landscape in about 1977. In the case of *A. nigrescens*, this extended period of recruitment from 1943 to 1977 was structured into short episodes. Recruitment was discontinuous at the landscape scale on both short and long time scales.

Fire and herbivore density records are not long enough to be really useful for interpreting causes of sapling release in this species. However, the end of recruitment in about 1977 was concurrent with dramatic increases in herbivore densities, particularly of mixed feeders like impala (*Aepyceros melampus*) and with the end of fire suppression throughout the range of *A. nigrescens* in the park. Fire frequencies remain low throughout the study area, however, and variations in fire frequency during the time covered by the dataset do not seem to affect recruitment rates of *A. nigrescens*.

Again, a non-parametric Kruskal-Wallis ANOVA was used to determine whether the timing of recruitment differed among hillsides because of unequal variance among hillsides and non-normal distributions (see Figure 6.9). Recruitment occurred at different times and with different intensities depending on location within the landscape (H=56.8, p<0.0001). Recruitment began earlier and occurred over a much longer time period on one hillside (Anig3) than on the others (Anig1, Anig2, Anig4, Anig5), evidence of

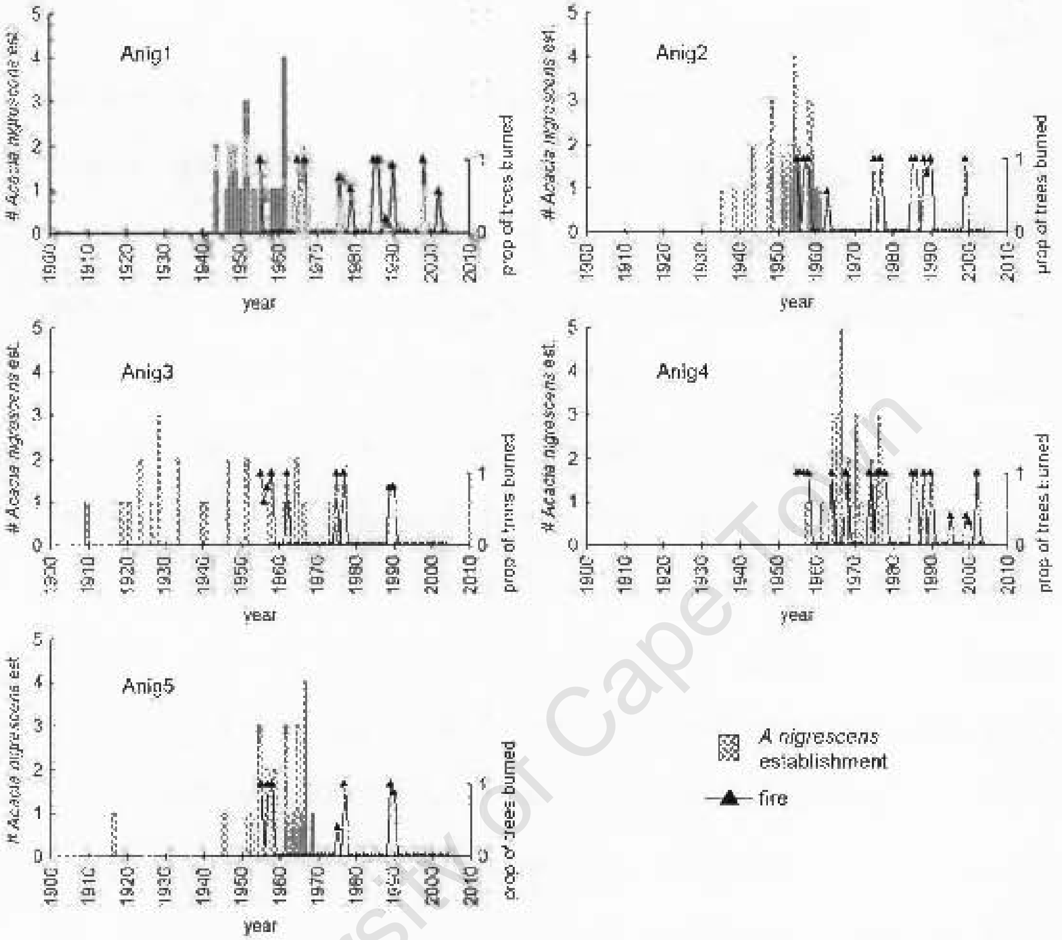

Figure 6.9. Timing of recruitment of adult *A. nigrescens* on five hillsides in Hluhluwe iMfolozi Park. Recruitment occurred during a short period or episode on some hillsides (Anig1, Anig2, Anig4, Anig5) and over time on others (Anig3). Fire frequency apparently did not impact on recruitment. Differences in ages of adults on these hillsides were significant (K-W ANOVA: H=56.8; $p<0.0001$).

discontinuous and heterogeneous recruitment. Of the hillsides that recruited over a short period, trees on two hillsides (Anig4, Anig5) recruited substantially later than trees on the other two (Anig1, Anig2). On one hillside (Anig5), the establishment of one tree approximately 30 years before the rest confirms that there were major gaps in recruitment. Comparisons with local fire histories indicated that fire did not occur with enough frequency to be a major determinant of rates of recruitment of *A. nigrescens* adults. Unfortunately, long-term local herbivore density estimates were not available.

Ages of adult *A. nigrescens* also differed significantly among stands (H=85.3, p<0.0001) (see Figure 6.10). Some hillsides had even-aged stands across the entire hillside or had trees with more variable age across the entire hillside (Anig1, Anig2, Anig4, Anig5). However, one hillside also had substantial variation among stands within the hillside (Anig3). As with *A. karroo* and *A. nilotica*, there was some degree of spatial separation of cohorts at the stand scale.

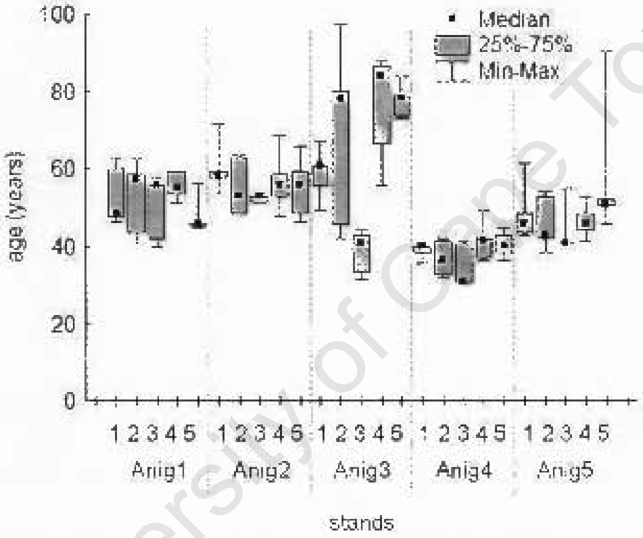

Figure 6.10. Ages of *A. nigrescens* adults in Hluhluwe iMfolozi Park. Medians, quartiles and ranges are presented for each stand of five trees. Five stands were sampled from each of five hillsides in the park. Hillside three (Anig3.1) demonstrated that recruitment of *A. nigrescens* was structured at the stand level. Differences in ages of adults in these stands were significant (K-W ANOVA: H=85.3; p<0.0001).

Recruitment of *A. nigrescens* is discontinuous at a landscape scale, but did not appear to be related to rainfall variability, herbivore densities, or fire history. Although recruitment did appear to end simultaneous with an increase in mixed feeder densities, defining and relating the timing of release to mixed feeder population growth would be speculative. *A. nigrescens* is variable at local/hillside and stand scales as well, suggesting that spatial variability in recruitment played a role in *A. nigrescens* population dynamics. At large scales, discontinuity in recruitment was characterized by a long period with a high frequency of year-long recruitment episodes, suggesting that there were cohorts even at large spatial scales. Cohorts of trees of the same age were also present at finer scales.

Discussion

We examined the population structure of three *Acacia* species (*A. karroo*, *A. nilotica*, and *A. nigrescens*) using tree ring aging of adult trees to determine whether establishment of adult *Acacia* trees is a continuous process at multiple scales: stand, hillside, and park. We compared population structure with records of rainfall, herbivore populations, and fire for evidence of recruitment related to, or limited by, variability in these factors.

SPATIOTEMPORAL PATTERNS IN *ACACIA* RECRUITMENT

Recruitment of adult trees was discontinuous for all species of *Acacia* included in this study. However, patterns of recruitment through time varied among species. *A. karroo* adults all established during a four year period of relatively low rainfall, high grazer and mixed feeder densities, and little fire, suggesting a landscape-scale episode. However, factors allowing sapling release functioned at finer scales, since timing of recruitment differed among hillsides and stands and occurred during periods when individual hillsides did not burn. Fire was the direct trigger for recruitment of *A. karroo*, but a drought and large grazer and mixed feeder populations probably contributed to decreases in fire frequency in the entire landscape. Low rainfall results in decreased grass growth and fuel-loads (Balfour & Howison 2001; Knapp *et al.* 2001), and high mixed feeder and grazer densities result in more intense grazing pressure and accompanying decreases in fire frequency and intensity (van Langevelde *et al.* 2003; Archibald *et al.* 2005; Collins & Smith 2006). Although isolating the effects of drought from the effects of grazing pressure was impossible, both probably contributed to a decrease in grass biomass and in fire frequency. We do not know if drought or increased grazing pressure alone would be sufficient to trigger sapling release and adult establishment. While climate is not within the control of management, managing herbivore densities around climate variation to maximize or decrease the possibility of an establishment event would be a possible component of managing tree populations and woody cover in these temporally dynamic savannas (see Westoby *et al.* 1989). In the case of *A. karroo*, management issues often center on preventing establishment of what is perceived to be a bush encroaching species (O'Connor 1995). Allowing herbivore populations to track rainfall more closely and to fluctuate and decline more severely during droughts and dry periods might allow some fire to continue burning during droughts and might prevent *A. karroo* establishment episodes from occurring.

Notably, *A. karroo* did not establish as adults during an earlier period with similar conditions – drought and high herbivore numbers – during the late 1970s and early 1980s. If it had, these adults should have still been in the landscape, if close to senescing (Gourlay *et al.* 1996). There are a number of hypotheses for why recruitment may not have occurred during this earlier period. The seedling or sapling bank that would have been released may not have been present in the landscape. Recruitment of saplings into adults depends on a sapling bank, than may in turn depend on a previous event or period with conditions suitable for seedling establishment (O'Connor 1995). Grasslands with *A. karroo* saplings were somewhat less common then than they are now, but were probably present in the landscape as early as the 1930s (see Chapter 3 in this volume; Henkel 1937; Whateley & Porter 1983). Alternatively, increasing atmospheric CO_2 concentrations may be allowing saplings to grow faster and to escape the fire trap more quickly than they could during the 1970s and 1980s (Bond & Midgley 2000). If this is the case, changes in atmospheric CO_2 are having major and tangible effects on tree dynamics in savanna systems.

A. nilotica and *A. nigrescens* adults recruited over a much longer period of time than *A. karroo*. *A. nilotica* adults recruited mostly between 1957 and 1965 and again between 1970 and 1975, and *A. nigrescens* between 1943 and 1977. Recruitment of both species declined to near zero in the mid-1970s, despite occupying different parts of the park with differing herbivore and fire ecology. Neither *A. nilotica* nor *A. nigrescens* shows any signs of recent or continuing recruitment. However, recruitment patterns within longer-term periods differed for *A. nilotica* and *A. nigrescens*. *A. nilotica* recruited continuously within its discontinuous but extended periods of recruitment, even for the most part at the hillside scale, although local patches of episodic recruitment did sometimes occur. By contrast, *A. nigrescens* recruitment rates were discontinuous from year to year, with especially high recruitment events every three to four years. Moreover, timing of recruitment of *A. nigrescens* differed more and was more episodic at the hillside and stand scale than *A. nilotica*.

Recruitment of neither *A. nilotica* nor *A. nigrescens* was obviously related to patterns in rainfall variability, herbivore densities, or fire frequency at the landscape scale, nor did either species appear to be constrained by fire at the hillside scale. However, the ecology of these two *Acacia* species may be linked directly to herbivory more than to fire. Bond *et al.* (2001) have suggested the short-grass landscapes dominated by grazers and mixed feeders favor *A. nilotica* more than the tall-grass, fire dominated landscapes that favor *A. karroo* (see also Chapter 3 in this volume). *A. nigrescens* occurs mostly in areas where herbivores are abundant and where fire has been historically rare; fire was suppressed throughout its range until 1955 and areas have burned only very infrequently since then. Unfortunately, local records of herbivore densities are unavailable and the accuracy and temporal resolution, even at the landscape scale, is poor, except for recent estimates. Examining the effects that local changes in herbivore densities may have had on recruitment of *A. nilotica* and *A. nigrescens* is impossible.

NON-EQUILIBRIUM IN SAVANNAS - IMPLICATIONS

High levels of variability in the age of these *Acacia* species indicate that woody cover and tree densities are not constant in these savannas, with major and frequent shifts in composition and dominance, at least in recent history. In mesic Hluhluwe, there appears to be turnover from *A. nilotica* to *A. karroo* dominance as bunchgrasses that favor *A. karroo* expand (see Chapter 3 in this volume; Archibald *et al.* 2005), and *A. nilotica* seems to be disappearing from the landscape. In iMfolozi, *A. nigrescens* woodlands have dominated the landscape apparently since at least the 1940s but have also stopped recruiting. We do not know what came before or what type of system will replace these woodlands as these large trees start senescing or are pushed over and damaged by elephants.

Neither tree structure, nor species composition, is stable in this savanna. The trees in this savanna and savannas in general are certainly variable systems not at equilibrium, but non-equilibrium is not easy to define (Ellis & Swift 1988; Illius & O'Connor 1999; Sullivan & Rohde 2002) and is therefore difficult to apply as a management principle. Many authors persist in using equilibrium concepts to frame savanna questions or to model tree-grass coexistence (Walker & Langridge 1997). Even work that uses variability in rainfall (Woodward & Beerling 1997) or fire and herbivory (Baxter & Getz 2005) often predicts some 'stable' or average vegetation state. Highly dynamic savanna tree dynamics present a challenge for savanna ecology and modeling: predicting vegetation that is structurally and compositionally variable in space and time.

The potential for major ecosystem changes driven by elephant damage to large trees is among the most pressing concerns in protected areas in Africa. However, models of elephant impacts on large trees often assume continuous recruitment of new large trees to replace ones damaged by elephants (Caughley 1976; Duffy *et al.* 1999), which simply does not occur. These models have the potential to seriously underestimate the impact of elephants on savanna systems. A demographic approach that uses tree population dynamics as a starting point (see Baxter & Getz 2005) and explicitly includes variability in tree recruitment is a necessary starting point for investigations of tree dynamics and tree cover in savannas.

However, shifts in dominance and species composition are a feature of savannas, with or without elephants. Monitoring elephant impacts on a few species of large tree, usually including *A. nigrescens*, would detect more change than predicted by elephant impact models, but elephants may only be accelerating changes occurring already. There may be less cause for concern than management and monitoring frameworks, like Kruger National Park's 'thresholds of potential concern' system, would lead us to believe.

Kruger in particular has adopted an adaptive management framework, after Westoby *et al.* (1989) (Rogers 2003). However, according to Gillson and Duffin (2007), the park's vegetation TPC states that woody cover should not fall to less than 80 percent of its highest ever value. These thresholds assume that we can and should conserve ecosystems in such a way that they at least broadly resemble their historical state. Our study shows that savannas have the potential to change in unexpected ways, with very little stability in either structure of species composition of the dominant trees and little continuity with historical conditions. Monitoring and management goals should also be structured more explicitly around a system dynamic that has the potential to be even broadly unpredictable.

Patch hierarchy theory suggests that this dynamic heterogeneity and shifting dominance at the local or regional scale forms part of a more stable matrix at regional to continental scales (Coughenour & Ellis 1993; Gillson 2004). In fact, the largest scale that we consider in the study is the park, and sampling sites are restricted to an area of approximately 300 km^2. Relative to the regional and continental scales at which stability in savanna ecosystems supposedly emerges, the largest scale considered here is fairly local. However, the regional landscape surrounding Hluhluwe iMfolozi Park is varied and diverse, bounded by the highveld and the Drakensberg to the north and west and by the Maputaland plain and the coast to the south and east (see Mucina and Rutherford 2006). Within this landscape context, and given high levels of compositional and structural savanna variability in the area, stability is unlikely to emerge at larger scale. Some savannas may be stable at regional and continental scales (Gillson 2004). Long-term studies of this kind in savannas are rare, and those that do exist conclude that savannas are meta-stable (Gillson 2004). Tree ring analyses in savannas (Prins & van der Jeugd 1993) and in conifer forests (Abrams & Orwig 1996; Bergeron 2000) have documented variable and episodic tree recruitment but stop short of concluding large-scale ecosystem instability. A dynamic tree layer, with shifting structure and species composition, that characterizes this savanna may be exceptional; the extent to which Hluhluwe iMfolozi Park can be used as a model and generalized for other savanna ecosystems is not clear. However, if this dynamic instability is a feature of savannas in general, their regional persistence and apparent meta-stability becomes still more of a puzzle. Explicitly considering non-equilibrium dynamics in savannas becomes fundamental to understanding their functioning.

Chapter 7

Synthesis

A. Carla Staver

SUMMARY

Variability in fire, herbivory, and climate facilitate the coexistence of trees and grasses in savannas (Scholes & Archer 1997; Higgins *et al.* 2000; Sankaran *et al.* 2004) and impact upon savanna structure (Belsky 1984; Prins & van der Jeugd 1993; Moreira 2000; Archibald *et al.* 2005; Sharam *et al.* 2006), which can also vary substantially both spatially and temporally (Gillson 2004). Fire (Bond *et al.* 2005; Sankaran *et al.* 2005) and herbivory (Prins & van der Jeugd 1993; Barnes 2001; Augustine & McNaughton 2004) can act to suppress tree growth and reduce woody cover below its potential maximum, according to regional average climate. Climate variability is also often thought to limit tree establishment (O'Connor 1995; Wiegand *et al.* 2004). Although these features can shape savannas at an ecosystem and even at a global level (Bond 2005; Bond *et al.* 2005; Sankaran *et al.* 2005), fire, herbivory, and climate variability limit tree cover via demographic controls on tree populations, usually by suppressing establishment or growth and maturation of tree saplings (Prins & van der Jeugd 1993; Hoffmann 1999; Higgins *et al.* 2000; Barnes 2001; Wiegand *et al.* 2004).

Tree distribution & community assembly

I examined the effects of herbivory and fire on *Acacia* sapling distribution (see Chapter 3). Distributions of saplings of seven *Acacia* species were structured by intensity of herbivore use and fire frequency, as well as by grass biomass and cover (see Figure 3.5). Species co-occurrence was not random, and intensity of herbivore use and fire were also good predictors of *Acacia* sapling community assembly (see Figure 3.7 and Table 3.4). However, herbivore use and fire frequency did not structure adult *Acacia* distributions as consistently (see Figure 3.6). In addition, saplings and adults of the same species often co-occurred, indicating a degree of stability; dispersal appeared to be limiting only for some species.

In addition, sapling branching architecture, which can be adapted for surviving herbivory and fire (Gignoux *et al.* 1997; Archibald & Bond 2003), was predictably related to a species niche along fire frequency and herbivore use gradients (see Figure 3.8). I conclude that fire and herbivory are major constraints on distributions of *Acacia* species via their effects on *Acacia* saplings, and saplings are adapted to surviving these disturbances.

Sapling growth

I also investigated the direct effects of browsing and a grazer-fire interaction on *Acacia* seedling establishment and sapling growth and mortality using data from a series of herbivore exclusion experiments (see Chapter 4). Major effects of herbivory and fire were on sapling growth rather than on seedling establishment or sapling mortality. Saplings responded to reductions in browsing intensity or no fire with increased growth (see Figure 4.3 and 4.6). This suggests a demographic bottleneck by browsing or fire that suppresses saplings; saplings recruit to adults when they are 'released' from intense pressure from browsing or fire (see Higgins *et al.* 2000).

Browsing and fire together were necessary to suppress sapling growth in mesic environments, where growth rates were higher, regardless of the intensity of herbivore use (see Figure 4.3). In semi-arid environments, where growth rates were slower, browsing or fire alone was sufficient to suppress sapling growth (see Figure 3.6). Tradeoffs between grazing intensity and fire intensity were evident in all parts of the landscape, but had a more pronounced effect on saplings in semi-arid environments.

I conclude that browsing has the potential to limit sapling growth and adult tree recruitment in savanna landscapes (see also Belsky 1984; Prins & van der Jeugd 1993; Barnes 2001; Augustine & McNaughton 2004), not only in small areas where browsing is particularly intense. Herbivory can also impact on savanna structure via decreased fire frequency and intensity in the presence of grazers (see also Archibald *et al.* 2005; Collins & Smith 2006). Temporal variability in herbivory, resulting locally from shifts in herbivore landscape use (Coughenour 1991; Bailey *et al.* 1996) or on a landscape scale from varying herbivory population size (Young 1994), probably shapes the way herbivores impact on tree populations. Intense herbivory limits sapling growth and tree recruitment until herbivory decreases, releasing saplings and allowing them to recruit into adults (see also Prins & van der Jeugd 1993).

Temporal and Spatial Variability in Impacts of Fire & Herbivory

Chapter 3 and Chapter 4 suggested that fire and herbivory suppress sapling growth and prevent them from establishing as adults, and that spatial and temporal variability in fire and herbivory determine sapling responses. I explicitly examined patterns of recruitment of adult trees of three species of *Acacia* over the past century at multiple spatial scales using dendrochronology. I then compared adult *Acacia* recruitment patterns to variability in rainfall, fire frequency and herbivory. *Acacia* adult recruitment was highly variable for all species. *A. karroo* recruitment occurred recently during times when fire frequency decreased locally (see Figure 6.3). However, local decreases in fire frequency occurred during a landscape scale drought and concurrent increase in herbivore densities. Fire varies with rainfall (Balfour & Howison 2001; Knapp *et al.* 2001) and intensity of herbivory (Achibald *et al.* 2005; Collins & Smith 2006); and landscape level interactions among all three influenced tree recruitment.

Recruitment of both *A. nilotica* and *A. nigrescens* seemed to have stopped entirely (see Figure 6.5 and Figure 6.8), indicating that this savanna was characterized by major shifts in dominance among *Acacia* species. Neither structural nor compositional dominance was stable in this savanna through time. Moreover, because this park is unique within a heterogeneous regional landscape, equilibrium is unlikely to emerge at a larger scale. Hierarchical patch theory (Coughenour & Ellis 1993; Gillson 2004) is unlikely to apply. Although the extent to which these patterns are generalizable to other savanna systems is unclear (see Gillson 2004), these results do suggest that using equilibrium-based models for savannas is inappropriate.

MANAGEMENT IMPLICATIONS

Biodiversity Conservation

Differentiation of acacias along herbivore use intensity and fire frequency gradients yields an ecologically diverse suite of species, with adaptations for success in diverse savanna systems (see Chapter 3). This diversity presents a unique and exciting challenge, particularly for conservation in savanna systems. Savanna ecology has often focused on savanna structure and on optimizing productivity, especially in rangelands. However, in conservation areas, the focus is less on productivity and more on biodiversity conservation. Our understanding of the biodiversity value of heterogeneous savannas and their disparate elements is developing (Pickett *et al.* 2003; Rogers 2003; du Toit 2003; van Wilgen *et al.* 2003).

Grazing lawns in particular have long been considered 'overgrazed', damaged systems because they were viewed from a productivity standpoint (Westoby 1985; McNaughton 1986), even though grazing lawns are often productive systems (Frank *et al.* 1998). Recent work has shown that grazing lawns provide a necessary resource for large mammal assemblages (McNaughton 1984; Bond & Archibald 2003; Verweij *et al.* 2006; Waldram *et al.* 2007) and host an endemic fauna, including birds (Krook *et al.* 2007) and spiders (Mandisa Mgobozi & Michael Somers, unpublished data). My study shows that grazing lawns also support distinct assemblages of *Acacia*, as well.

The fundamental dependence of savanna heterogeneity on disturbances like fire and herbivory and on the dynamic grass layer means that management of these dynamic elements can have an impact on biodiversity. In Hluhluwe iMfolozi Park, where this work was conducted, grazing lawns were long considered to be degraded and management focused on 'restoring' them to tall bunch grasslands (Mentis 1968; Brooks & McDonald 1983). Grazing lawns are under threat and are probably much rarer than they were historically (Frank *et al.* 1998; Bond *et al.* 2001); the tree species that recruit on grazing lawns are more widespread as adults than as saplings (Bond *et al.* 2001). Fire-adapted bunch grasses cover most of the landscape (Archibald *et al.* 2005) to the point that fire-adapted species, especially *A. karroo* and *Dichrostachys cinerea*, are major bush-encroaching species throughout southern Africa (O'Connor 1995; Roques *et al.* 2001). In addition, *Acacia* seedlings and life-cycles seem to depend on disturbances from either herbivory or fire; open *Acacia* savannas may be eliminated entirely and replaced by broad-leaved thicket by fire and herbivore suppression (Smith & Goodman 1986; Smith & Goodman 1987; Sharam *et al.* 2006). Conservation areas need to focus explicitly on biodiversity conservation in heterogeneous savannas (Rogers 2003), to acknowledge the functional role of herbivory and fire, and to develop fire and herbivore management strategies that promote a diversity of savannas.

Savanna Structure

Both browsing and fire act on *Acacia* saplings to suppress growth and prevent maturation of saplings to adults (see Chapters 4 and 6) and have the potential to limit tree cover and tree establishment in savannas (Prins & van der Jeugd 1993; Scholes & Archer 1997; Roques *et al.* 2001; Bond *et al.* 2005; Sankaran *et al.* 2005). While the potential role of fire in limiting woody cover and shaping savanna physiognomy has been widely acknowledged (Higgins *et al.* 2000; Bond *et al.* 2005; Sankaran *et al.* 2005) and the use of fire as a management tool is widespread (Biggs & Potgeiter 1999; van Wilgen *et al.* 2000; Govender *et al.* 2006), the impacts of herbivory are not as easily generalized. Acknowledging the potential for browsing, in particular, to directly control woody cover would allow us assess the extent of the impacts of herbivory on woody cover. In this study, browsing imposed strong controls on sapling growth in semi-arid environments, but even in mesic environments, fire was able to prevent sapling escape only in conjunction with browsing (see Chapter 4). Bush encroachment is a major concern in savannas worldwide (Archer 1990; O'Connor 1995; Brown & Archer 1999; Roques *et al.* 2001). In systems with extant browser assemblages, levels of browsing could potentially be managed to prevent or at least to mitigate against extensive bush encroachment into savannas.

However, managing the impact of fire and herbivory on tree populations and on savanna structure requires a context-specific understanding of how fire and herbivory interact with each other and with variable climate. Recruitment of *A. karroo* adults depended on a lull in fire frequency, but a landscape-scale drought and increase in herbivore numbers contributed to that decrease in fire frequency (see Chapter 6). Opportunistic management of fire and herbivory around major climatic events, contingencies, and other major temporal changes in savannas, such as rising levels of atmospheric CO_2 (Bond and Midgley 2000), should form a part of long-term management strategies (Westoby *et al.* 1989).

Even opportunistic management around contingencies must be structured around explicit conservation goals. However, setting goals in variable savannas, which have the potential to change in unexpected ways, with very little stability in either structure of species composition of the dominant trees and little continuity with historical conditions (see Chapter 6), presents a new set of challenges for managers. Even the 'thresholds of potential concern' (TPCs) employed by Kruger National Park in South Africa, widely touted as a move away from equilibrium-based management, are based upon a fundamental equilibrium, around which system characteristics fluctuate (Gillson & Duffin 2007). These thresholds assume that we can and should conserve ecosystems in such a way that they at least broadly resemble their historical state. These indicators or thresholds are an important feature of a monitoring system, but should not form the main-stay of a management plan. Adaptive management incorporates monitoring, but emphasizes flexibility over fixed policy and uses experimental management to determine potential transitions and outcomes (Westoby *et al.* 1989). Management structures need to be more flexible and dynamic in order to deal with highly variable systems.

FUTURE RESEARCH

How effective is architecture?

This study showed that *Acacia* species distributions are structured along fire frequency and herbivore use gradients, and that sapling branching architecture was predictably related to the position of species along those gradients. Species that occurred in areas with frequent fire and low herbivore use formed poles, while species that occurred in areas with infrequent fire and intense herbivory formed cages (Chapter 3; see also Gignoux *et al.* 1997; Archibald & Bond 2003). The degree to which these strategies improve saplings' ability to survive fire or to avoid or tolerate herbivory is unknown. Recent work has shown that *A. karroo* saplings resprout from stored root reserves repeatedly after fires and that the Hluhluwe form of the species has a life-history uniquely adapted to occupying a frequent-fire niche (Schutz 2007). However, the effectiveness of a highly-branched architecture in deterring herbivory by changing feeding behavior and decreasing feeding efficiency (see Illius *et al.* 2002) has been little studied.

Can browsing control woody cover on a global scale?

Fire and browsing both suppress tree growth (Higgins *et al.* 2000; Barnes 2001; Augustine & McNaughton 2004; Schutz 2007) and contribute to heterogeneity in savanna structure (Eckhardt *et al.* 2000; Moreira 2000; du Toit 2003; van Wilgen *et al.* 2003; Redfern *et al.* 2005; D'Odorico *et al.* 2006). The global influence of fire in suppressing tree cover below its potential 'climate maximum' has been well documented (Bond *et al.* 2005; Sankaran *et al.* 2005), but the global influence of herbivory has not, probably because it is more difficult to generalize. However, translating the effects of herbivory on sapling growth, which are substantial, into effects of herbivory on woody cover requires at least a regional-scale assessment of woody cover related to herbivory.

Refining *Acacia* Dendrochronology

The *Acacia* dendrochronology used in this study (see Chapters 5 and 6) enabled a long-term analysis of tree recruitment that would have been otherwise impossible. However, age estimates were only within ±1 year for *A. karroo*, within ±4 years for *A. nilotica*, and just over ±5 years for *A. nigrescens* (see Chapter 5). Given these levels of estimation error, differentiating between short recruitment events and longer periods of recruitment was impossible, and more accurate age estimates might yield a better understanding of the types of events that shape savanna landscapes. Temperate dendrochronology relies heavily on measuring ring width as well as counting rings and cross-referencing these ring-widths with standards and with climate records (Fritts 1976; Schweingruber 1996). The *Acacia* trees aged for this study did not form even and concentric rings, as temperate trees do, making measurements of ring-width meaningless. However, I attempted some preliminary analyses that indicate that relating ring cross-sectional area (CSA) to climate variability might be fruitful.

A clearer understanding of the physiology of ring formation and the circumstances under which rings form is necessary as a starting point for linking ring CSA to climate. We do know that rings are bands of marginal parenchyma that sometimes, although not always, contain chains of calcium oxalate crystals (Gourlay & Grime 1994; Gourlay 1995). Some studies have attempted to validate ring counts as a method for estimating tree age using cambial injury techniques (see Wyant & Reid 1992); cambial injury might also be used to establish timing of ring formation in relation to current known climate history.

Linking Tree Rings to Climate, Fire and Herbivory

Linking recruitment of *A. karroo* to rainfall, fire frequency and herbivore use was possible because age estimates were relatively accurate and because adults recruited relatively recently, when rainfall, fire, and herbivore population records were reliable. However, I was unable to relate recruitment of *A. nilotica* and *A. nigrescens*, possibly because age estimates were less accurate and because rainfall, fire, and herbivore population records were of poorer quality over the longer term. There is potential for age estimates from ring counts for *Acacia* trees to improve.

Stable isotopes in tree rings have also been used to link tree growth to climatic variation, using $\delta^{18}O$ and $\delta^{13}C$ (McCaroll & Loader 2004), and to changes in nitrogen cycling patterns, using $\delta^{15}N$ (Poulson *et al.* 1995), which are related to fire and herbivory in savanna ecosystems. Stable isotopes could potentially be used to examine timing of recruitment of *Acacia* and other tree species relative to environmental conditions at the time of recruitment.

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