The differences in grass species composition and the effects on fire behaviour in an African mesic savanna

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Abstract

Fire is a key determinant of savanna dynamics, particularly with respect to its influence on vegetation dynamics. The grass species composition and structure of savannas have impacts on fire behaviour through their differing fuel characteristics related to each species specific phenologies and morphologies. Climate change and elevated atmospheric CO_2 levels may influence the trajectory of grassy ecosystems over a large spatial and temporal scale. These dynamics operate through to competition between C_4 and C_3 plant, where C_3 plants have a competitive advantage under conditions of elevated atmospheric CO_2 levels. This competitive advantage may be mitigated by landscape scale disturbances, including fire and small disturbances, such as game trails created by animals. Different grass clades appear to differ in productivity and moisture content with Andropogoneae (*Themeda triandra* and related species) being highly productive, but drying out early after exposure to drought compared to Paniceae (*Panicum maximum* and related species), which holds moisture for longer in the dry season. This study begins to delve in how these processes interact in these grassy mesic savanna ecosystems. The focus of this study is upon the differences in the fire ecology of grasslands dominated by *Themeda triandra* (*Themeda*) and *Panicum maximum* (*Panicum*) and the effects that game trails surrounding thicket patches have on fire continuity and spread.

From a fire perspective, fuel load and moisture content are major contributors to fire spread. Grass biomass contributing to fuel was found to differ between the two respective dominant grass species. *Themeda* (5000-6500 kg/ha) had significantly higher fuel loads than *Panicum* (3000-4000 kg/ha) ($p<0.001$). The fuel moisture content of *Panicum* was significantly higher than the moisture content of *Themeda*, where the latter cured more rapidly than the former through the dry season ($p<0.001$). Therefore, rates of curing *Panicum* swards were influenced by season ($p<0.01$). It is postulated that these differences would affect the fire behaviour in an African mesic savanna. The experimental fires were affected by the timing in the dry season of the fires ($p=0.03$), the grass species composition ($p=0.02$) and the grassy fuel loads ($p<0.001$). The rates of spread of the fires increased with increasing fuel loads ($R^2=0.71$). There were higher fire intensities in grasslands dominated by *Themeda* (~5500 kW/m) than observed in grasslands dominated by *Panicum* (~2000 kW/m) ($p=0.01$). *Themeda* swards were able to burn with high fire intensities at any time in the dry season, whereas swards dominated by *Panicum* burnt more intensely later on in the fire season. Animals were able to

impact the behaviour of fire, not only through herbivory, but through the creation of game trails around thicket patches. The presence of these trails around thicket patches were able to impede fire continuity and spread, thus "protecting" thicket patches ($p<0.001$). This was enhanced by the grass species composition around the thicket edges being largely dominated by *Panicum*; this may create an "edge effect" that could mutually reinforce the "game trail" effect in protecting thicket patches.

Changing climate and elevated CO_2 conditions and disturbances through fire and animals may affect the species composition, structure and functioning of mesic savanna landscapes. Managers of African savannas can manipulate fire intensity by choosing the time in the season to burn, and further by burning in years with higher or lower fuel loads. If the management objective were to maintain savannas dominated by C_4 grasses, then the management protocol would be to use of frequent, high intensity fires that may provide C_4 plants with a competitive advantage over C_3 plants and mitigate the spread of C_3 plants into the now C_4 dominated systems. This may be able to restrict the encroachment of woody species typical of the savanna thicket stable state in open savannas that has become an increasing phenomenon in these landscapes.

Declaration

I know the meaning of plagiarism I, the undersigned, hereby declare that this thesis is the result of my own original work, except where otherwise indicated and acknowledged, and that it has not been submitted for a higher degree in any other university.

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Cameron Wills

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Table of contents

Abstract.....1

Declaration.....3

Acknowledgements.....4

List of figures.....7

List of tables.....9

Chapter 1: Introduction

Disturbance regimes in mesic savannas.....10

Fire and grass species composition.....14

Mammal herbivory and fire spread.....15

Key questions.....16

Study Area.....18

Chapter 2: Grass species composition and phenology

Introduction.....22

Methods.....25

Results.....28

Discussion.....32

Chapter 3: Grass species composition and fire behaviour

Introduction.....36

Methods.....37

    Experimental fires.....37

Fire Models..40
Results
Contributions to fire intensity...42
Contributors to fire intensity of *Themeda triandra* and of *Panicum maximum*....45
Fire intensity models 49
Discussion..51

Chapter 4: The animal impact

Introduction...57
Methods...58
Results...61
Discussion...66

Chapter 5: Synthesis...69

References...75

Appendices..89

List of Figures

Figure 1.1: The percentage dominance of grasses, forbs and bare ground in recovering thicket areas after an extreme fire event in 2008 in HiP

Figure 1.2: Aerial photograph of Manzibomvu hill in HiP in the dry season. The fire plots were oriented perpendicular to the paved road with each plot stretching from the road to the upper hill slopes. The lower slopes were dominated by *Themeda triandra* (reddish brown) and upper slopes by *Panicum maximum* (white)

Figure 1.3: Layout of study sites on Manzibomvu hill in HiP
Figure 1.4: *Themeda triandra* (left) and *Panicum maximum* (right)
Figure 2.1: recorded vegetation types at Manzibomvu hill in HiP in 1937 from Henkel (1937)

Figure 2.2: Dimensions and transect layout in a single experimental plot from the Manzibomvu hill study area

Figure 2.3: the frequency (%) of the dominant species in the *Panicum maximum* grass sward for 2013 and 2014 of 70 DPM measurements per plot, thus 840 DPM measurements over the two years

Figure 2.4: the average grass biomass present in all of the plots dominated by *Themeda triandra* or *Panicum maximum* for 2013 and 2014

Figure 2.5: the percentage grass curing from April to August of *Themeda triandra* (*Themeda*) and *Panicum maximum* (*Panicum*) in 2013, (+SE)

Figure 2.6: the percentage grass curing from April to July of *Themeda triandra* (*Themeda*) and*Panicum maximum* (*Panicum*) in 2014, (+SE)

Figure 3.1: the fire protocol for igniting fires in each subplot of *Themeda* and *Panicum* per plot at different times in the fire season

Figure 3.2: the difference in fire intensity of all fires of *Themeda triandra* (*Themeda*) and *Panicum maximum* (*Panicum*) for 2013 and 2014

Figure 3.3: The average fire intensities experienced in *Themeda triandra* swards and *Panicum maximum* swards compared to the flame heights observed at different times in the fire season for 2013 and 2014

Figure 3.4: The average fire intensity recorded per experimental fire treatment for *Themeda triandra* (*Themeda*) dominated grasslands and *Panicum maximum* (*Panicum*) dominated grasslands during the fire seasons in 2013 and 2014

Figure 3.5: the relationship between rates of spread and fuel biomass for *Themeda triandra* dominated grasslands

Figure 3.6: Regression analysis of the relationship between relative humidity and fire intensity for *Panicum maximum* dominated grasslands

Figure 3.7: the relationship between rates of spread and fuel biomass for *Panicum maximum* dominated grasslands for each site

Figure 3.8: Regression analysis showing the observed fire intensities against the predicted fire intensities from the Trollope and Trollope (2002) fire intensity model

Figure 3.9: Regression analysis showing the observed fire intensities against the predicted fire intensities from the BehavePlus5 fire behaviour model

Figure 4.2: An illustration of the study sites where there was a trail present and when there was no trail present on Manzibomvu hill

Figure 4.3: The estimates of burn severity in the quadrats for each treatment

Figure 4.4: The average biomass present in the grassland leading up to the thicket and the average biomass in the ticket areas for the treatments, trail present and no trail present

Figure 4.5: The overall grass species composition (frequency %) in the grassland leading up to the thickets for both treatments

Figure 4.6: the overall grass species composition in the thickets for both treatments (frequency %)

Figure 4.7: the frequency (%) of the grassland leading up to the thicket that did or did not burn for the treatments, trail present or no trail present

Figure 4.8: the frequency (%) of the thicket that that did or did not burn for the treatments, trail present or no trail present

List of Tables

Table 2.1: Percentage species composition in each plot dominated by either *Themeda triandra* or *Panicum maximum* in 2013 and 2014

Table 2.2: A general linear model for grass curing of *Panicum maximum* and *Themeda triandra* for 2013 and 2014

Table 3.1: A general linear model for factors contributing to the differences in fire behaviour of grass swards across different times in the fires season for all fires

Table 3.2: A general linear model for the factors affecting the variation in fire behaviour for *Themeda triandra* swards and *Panicum maximum* swards across the different times in the season for 2013 and 2014

Table 3.3: A comparison of the fire intensity for the BehavePlus5 model and the Trollope and Trollope model against the observed values obtained from the experimental fires

Table 3.4: Comparative fuel load and fire intensity data from savanna vegetation in Africa and Australia

Table 4.1: A GLM for whether the fire was able to burn into the thicket for the treatments, trail present and no trail present

Table 4.2: The number of times the fire did or did not burn into the thickets for the treatments, trail present and no trail present

Appendix 1: The dates, times and weather conditions of each of the fire treatments
Appendix 2: Summary of the average fire behaviour outputs for each species at different times in the fire season
Appendix 3:BehavePlus5 model parameters used for simulation of fire behaviour (data from van Wilgen and Wills, 1988)

Appendix 4: The average biomass present in each sub-plot of *Themeda triandra* and *Panicum maximum* at different times in the fire season used in the simulation of fire behaviour in the Trollope and Trollope fire intensity model and the BehavePlus5 model

Chapter 1: Introduction

Savannas are complex ecosystems and it is a challenge to understand the factors that govern their distribution, structure and functioning. Multiple interacting factors affect the dynamics of these ecosystems including, climate, hydrology, herbivory, fire and soil characteristics that can all influence the distribution of savanna (Tinley, 1982; Furley, 1992; Hopkins, 1992; Ruggiero *et al*., 2002; Bond, 2008, Lehmann *et al.,* 2011).

Disturbance regimes in mesic savannas:

Atmospheric concentrations of carbon dioxide (CO_2) have varied greatly over the long geological timespan covering the evolution of terrestrial plants (Royer *et al*, 2007; Beerling and Royer, 2011). A drop in CO_2 concentrations to well below 500ppm is thought to have triggered the development of the C_4 photosynthetic pathway, which is currently the dominant physiology of grass species typically dominant in open savannas (Cerling *et al.,* 1997; Christin *et al*., 2008; Edwards *et al*., 2010). Grass species with C_3 and C_4 photosynthetic pathways differ in physiology, anatomy and ecological responses (Pearcy and Ehleringer, 1984; Ripley *et al*., 2010). C_4 photosynthesis is a set of anatomical and physiological adaptations concentrating CO_2 around the photosynthetic enzyme – Rubisco, which under conditions of high temperatures and low atmospheric CO_2 concentration raises photosynthetic efficiency in C_4 species relative to C_3 species (Bjorkman, 1970; Ehleringer *et al*., 1997; Sage, 2004; Balfour and Midgley, 2009). Therefore, CO_2 assimilation rates are typically higher in C_4 plants than in C_3 species under high light, warm growing season temperatures and where atmospheric CO_2 is well below 500ppm (Long, 1999; Balfour and Midgley, 2009).

Atmospheric CO_2 concentrations have risen from some 280ppm to 400ppm since the advent of the industrial revolution in the mid-19th century. Historical atmospheric CO_2 concentrations measured in air bubbles trapped in glacial ice cores ranged from ~170 ppm to ~300 ppm over the last 800 thousand years with a similar range of concentration levels extending back for several million years (Petit *et al*., 1999; Luthi *et al*., 2005; Honisch *et al*., 2009).Thus current atmospheric CO_2 concentration levels are approximately 40% greater than maxima recorded for millions of years – and are continuing to climb. Besides contributing to global warming, the atmospheric CO_2 concentration increase is likely to fundamentally shift competitive dynamics among plant species with different physiological characteristics and photosynthetic pathway adaptations and thereby impact the structure and composition of ecosystems and their ecological functioning.

Research on the evolution and expansion of C_4 plant species suggests that both climate and atmospheric CO_2 concentration are critical determinants of their potential competitive advantage and ultimately the distribution of C_4 grasses (Ehleringer *et al.* 1997, Collatz *et al.* 1998, Osborne 2008). Increasing atmospheric CO_2 concentration favours C_3 plants (Ehleringer *et* al, 1997; Collatz *et al*, 1998; Chamaille-Jammes and Bond, 2010), while global warming is expected to favour C_4 plants (Sage and Kubien, 2003). Although the ecological implications of future C_3/C_4 shifts have received little attention, predictive modelling indicates a delay in the rate at which C_4 dominated grasslands are likely to contract, due to intrinsic time-lags. Some authors suggest that environmental conditions, such as seasonal water availability (Winslow *et al.,* 2003), soil nutrient and water status levels (Belsky *et al*., 1989) or fire regimes (Keeley and Rundel, 2005) may alter the trajectory of the predicted change from C_4 to C_3 species dominance (Sage and Kubien, 2003). Based on their quantum yield model, Collatz *et al.* (1998) predicted that C_4 grasses would have covered more than half of the world's vegetated land surface at the low CO_2 levels characteristic of the last glacial period, despite the low temperatures. They predict that C_4 grasses will shrink to a small fraction of the land surface area under current and future elevated atmospheric CO_2 concentration levels, less than 10%, when atmospheric CO_2 concentrations reach about 700ppm (perhaps by the end of the century) despite global warming. Initially, rising atmospheric CO_2 concentrations may contribute to an increase in C_3 woody plant encroachment and changes in C_4 grass species composition with implications for fire spread. In turn, this may lead to the increasing dominance of shade tolerant grasses. As atmospheric CO_2 concentrations continue to rise, C_3 plants may become more prominent in grassy biomes by out-competing C_4 species, over the longer-term.

Currently C_4 grasses are dominant in grasslands and savannas in the lower latitudes, which cover about 20 percent of the land surface area (Bond, 2008; Bond and Midgley, 2012). However, C_3 woody plant expansion has become an ever increasing phenomenon within grassland and open savanna biomes over the last century, creating an ever increasing canopy cover of trees in these ecosystems. This is particularly the case for grasslands and savannas, where C_4 grasses might compete with C_3 woody or grass species (Ehleringer *et al*., 1997; Collatz *et al.*, 1998; Bond and Midgley, 2000; Sage and Kubien, 2003; Chamaille-Jammes and Bond, 2010).

In African mesic savannas, the underlying large-scale disturbance regime of elevated atmospheric CO_2 concentration and a changing climate favours the establishment of stable state closed thicket or woodland habitats. Under these conditions, the persistence of more open and C_4 species dominated savannas depends upon various spatial and temporal scale disturbance regimes (Delcourt and Delcourt, 1988; Morgan *et al.*, 1994; Millar and Woolfenden, 1999). The lower woody biomass in savannas relative to their climate potential is assumed to be due to medium-term and landscape-scale disturbance regimes, such as fire. and short-term and smaller site-specific scale disturbance regimes such as herbivory and other animal impacts, or the interaction between the effects of these disturbances (Higgins *et al*., 2000; Asner *et al*., 2004; Sankaran *et al*., 2005; Archer, 2007, Bowman *et al.,* 2008). A conceptual framework for understanding how these interact to determine the limits of the savanna biome is an area of active research (Lehmann *et al*., 2011).

Several researchers have studied interactions among trees and grasses in savannas. Trees create micro-environments that improve the water and soil nutrient status available for plants growing beneath their canopies (Belsky *et al*., 1989), resulting in different grass species predominating in the shade of the tree canopy to those in open grassland areas (Ellis, Vogel and Fuls, 1980; Belsky *et al*., 1989). In African mesic savannas, Kinyamario *et al.* (1995) observed that *Panicum maximum* (*Panicum*) is more dominant in shaded habitats, whereas, *Themeda triandra* (*Themeda*) is more dominant in open habitats. Downing and Marshall (1980) made a similar observation and postulated that the distribution of *Panicum* and *Themeda* might be controlled by grazing pressure and soil fertility. Although both *Panicum* and *Themeda* have a C_4 photosynthetic pathway, *Themeda* has the nicotinamide adenine dinucleotide phosphate (NADP) form of C_4 photosynthesis, with a higher quantum yield of efficiency under full-sunlight photorespiration conditions and lower atmospheric CO_2 concentrations. In comparison, *Panicum* has the phosphoenol pyruvate carboxykinase (PCK) form of C_4 photosynthesis which is less efficient under the same photorespiration and atmospheric CO_2 conditions (Seemann *et al.*, 1984; Ehleringer and Monson, 1993; Taylor *et al.,* 2010). In the C_4 dominated grasslands of South Africa and Australia, NADP and PCK grasses both exhibit positive correlations with increasing rainfall; however, NADP grasses were sensitive to increasing aridity (Hattersley and Watson, 1992; Ehleringer and Monson 1993; Visser *et al.*, 2012). This suggests that the different photosynthetic pathways that exist within the C4 clade may also have an impact on ecosystem functioning. The ecological behaviour of *Panicum* is analogous to that of a C_3 grass, as it tends to stay greener for longer in the dry season, which may influence its effects on fire behaviour. Chamaille-Jammes and Bond (2010) observed changes in C_4 to C_3 dominance in response to herbivory, and perhaps similar dynamics apply to how fires might have different ecological effects on grass swards dominated by different grass species.

Medium-term and landscape-scale disturbance regimes (such as fire) are a major determinant of structure and composition in grasslands (Stuwe and Parsons, 1977; Tremont and McIntyre, 1994; Briggs and Knapp, 1995; Lunt, 1997; Tainton, 1999). Landscape-scale fire disturbance regimes have been shown to be a primary determinant of these ecological dynamics within mesic savannah ecosystems (Bond and Van Wilgen 1996; Anderson, Cook and Williams 2003). Savannas are the world's most frequently burnt ecosystems (Archibold, 1995) and the relative abundance of species characterised by either the C_3 or C_4 photosynthetic pathways are related to the fire regime (Dillon, 1980; Bond and van Wilgen, 1996), with C_4 grass species dominating under conditions of frequent fire (Robinson *et al.,* 1979; Tix and Charvat, 2005; Bowman *et al.*, 2009).

Fire intensity affects tree and grass recruitment and tree mortality (Trollope, 1984; Govender *et al.*, 2006). Many long term fire experiments in African and other savannas have shown how variation in fire frequency and season influences tree species composition and canopy cover (O'Connor *et al.*, 2014). Complete fire suppression in mesic savannas results in its transition to a closed thicket/woodland/forest vegetation type (Bond *et al.* 2005; Bond, 2008, O'Connor *et al.*, 2014), which indicates that fire might be the dominant factor that controls the shift between grassland and closed woodland habitats in savannas. This effect of fire is especially strong in mesic savannas with more than 650 mm of annual rainfall (Sankaran *et al.*, 2005). Effects of fire include the reduction of biomass of dominant grasses, thereby enabling regeneration of small-statured herbaceous species (Morgan 1998) and reducing invasion of woody species (Adamoli *et al.*, 1990; Bond and Archibald, 2003; van Langevelde *et al.*, 2003; Briggs *et al.*, 2005; O'Connor *et al.*, 2014). Additionally, the prevalent fire regime plays a role in maintaining open grassland systems by creating conditions affecting competition between grasses and trees; and maintaining a particular balance between trees and grasses (Roques *et al.*, 2001).

These fire driven effects on ecosystem composition, structure and function create the opportunity to use fire as an effective land management tool (Trollope, 1983; Booysen and Tainton, 1984; Bond *et al*, 2003; Hirota *et al*, 2011; Lehman *et al*, 2011; Staver *et al*, 2011) to achieve specific goals set by land managers. These include the use of fire in managing bush encroachment and in controlling the time of burn in order to achieve either high intensity fires or low intensity fires. "Fire regimes" are specific patterns of frequency, season, intensity and type of fire (Gill, 1975), where season of fire, and possibly fire intensities, can be influenced (Govender *et al.*, 2006) and managed at a landscape-scale. Fire can be a particularly useful ecological management tool, applicable to both large (such as the Kruger National Park) and small landscapes.

Fire and grass species composition

Some studies that consider the effect of different plant types on the fire regime have focussed on the effects of plant species recruitments or dominance shifts. For example, in Neotropical and Australian savannas, introduced African pasture grasses have been shown to alter fuel load and increase both fire frequency and intensity thereby disrupting indigenous savanna structure and functioning (D'Antonio and Vitousek, 1992; Rossiter *et al.,* 2003). In contrast, woody species, such as *Chromolaena odorata* invading African and Asian savannas, often alter the fire regime by decreasing grass fuel load and fire frequency by out shading the grasses, but increase the risk of intense canopy fires (Brooks *et al.,* 2004; te Beest *et al.,* 2012). Ripley *et al.* (2010) compared the flammability of the South African grass *Alloteropsis semialata*, which has both C_3 and C_4 subspecies. They found that the C_4 subspecies had low amount of live above-ground biomass and high amount of dead above-ground biomass – having assigned most of their resources to below-ground living biomass - and consequently had higher and drier fuel loads that should result in increased fire frequencies and intensities.

In comparison, the C_3 counterpart retained 33% of their live above-ground biomass in the dry season, and was thus less flammable and less able to recover after fires. Based on these physiological differences the authors suggested that the C_4 sub species was better adapted to frequent fire with the capability to reallocate below-ground biomass resources in order to aid in post fire recovery, while the C_3 subspecies with a greater allocation of resources to above ground leaf area that is vulnerable to removal by fires, resulted in a less fire adapted growth form (Ripley *et al*., 2010).

Mammal herbivory and fire spread

Mammal herbivory and fire are the two major classes helping to shape African savannas, however, they have usually been investigated independently (Archibald *et al*., 2005). Mammal herbivores can reduce woody plant growth and reduce closed-canopy formations in savannas. Fire and grazing have been shown to influence vegetation composition (e.g., Tainton and Mentis 1984, O'Connor, 1994), annual aboveground net primary productivity (Milchunas and Lauenroth 1993, Knapp *et al*., 1998), and nutrient cycling (Hobbs *et al*., 1991, van de Vijver 1999). There are few studies that have focused on the interaction between fire and grazing (see Collins 1987, Belsky, 1992, Vinton *et al*., 1993 and Noy-Meir, 1995). The research gap is understandable when one considers the scale at which fire and grazing interacts and the logistical difficulties with manipulating fire and herbivory at a landscape scale (Archibald *et al*., 2005; Bowman *et al*., 2008). Fire affects grazing by altering large-scale foraging patterns and grazers affect fire by reducing fuel loads and altering fire spread in a landscape (Archibald *et al*., 2005). There have been studies in African savannas (Hobbs, 1996; O'Connor *et al*., 2011), Australian savannas (Leonard *et al*., 2010) and North American savannas (van Auken, 2000) that indicate the importance of heavy grazing in decreasing fire frequencies and intensities (Kimuyu *et al.,* 2014). This suggests that the role of mega-herbivores is crucial in disturbance-centred feedbacks in these ecosystems (Lehmann *et al*., 2011). Waldram *et al.* (2008) proposed that mega herbivores (White Rhinos) in Hluhluwe-iMfolozi Park act as ecosystem engineers, by creating and maintaining grazing lawns, which altered habitats for other grazers and changed the fire regime. The focus of changing the fire regime was largely on the effects of tall grasses versus short grasses. However, this thesis focuses on tall grasses only and shifts in their species composition.

Animal impacts have additional effects on fire spread, including the formation of natural firebreaks in the form of game trails. Walker and Heitschmidt (1986) suggested that intensive rotational grazing of cattle on rangelands affected the ecosystem in many aspects, one of which was the formation of cattle trails through hoof action. The cattle trails generally connected favoured grazing, resting and watering areas for the cattle. The trails were usually formed on routes of least resistance, such as the crests of ridges, in valleys and parallel to contour lines (Weaver and Tomaneck, 1951; Arnold and Dudzinski, 1978, Oikawa *et al.*, 1981).

There are similar disturbance structures that can be seen in African savannas. Large herbivores create game trails in savannas and around thicket edges that are used to move through and around the habitats. The effects of grazers on woody cover are indirect and usually considered to be mediated through reductions in fuel loads and thus fire frequency and intensity, as well as decreased competition (Van Auken, 2000; Asner *et al.*, 2004; Werner, 2005; Bowman *et al.,* 2008). However, game trails present in these systems can disrupt fuel continuity and hence the ability of fires to spread and propagate over large areas (Swetnam *et al.*, 1999). An example of this effect is illustrated in a statement by Arthur Noon, where he noted that the Huachucas were so full of cattle and cattle trails that the trails served as good fire breaks (Bahre, 1991; Swetnam *et al.*, 1999).

Key questions

In the late dry season of 2008 an extremely intense fire event occurred in the northern part of the Hluhluwe-iMfolozi Park, South Africa, which resulted in a firestorm that burned through much of the closed thicket vegetation in the mesic *Acacia* savanna open grassland/closed thicket mosaic predominant in the area. The 2008 firestorm episodic event together with subsequent fires in 2010 and 2012 created open grassland/forest/closed thicket mosaic vegetative landscape (Browne, 2009; Wills, 2012). Wills (2012) observed that *Panicum* became more prominent in the recovering thicket areas (figure 1.1). This 2008 firestorm event and the subsequent fire regime effectively created an opportunity to explore the effects of the landscape scale fire disturbance regime in grasslands dominated by different species, specifically, *Themeda* dominated grasslands in the open savanna areas and *Panicum* dominated grasslands in the recovering thicket areas. Further, it provided the opportunity to examine the interaction of this landscape scale fire disturbance regime with a game trail barrier site scale disturbance regime at the edges of remaining closed thicket patches in the landscape.

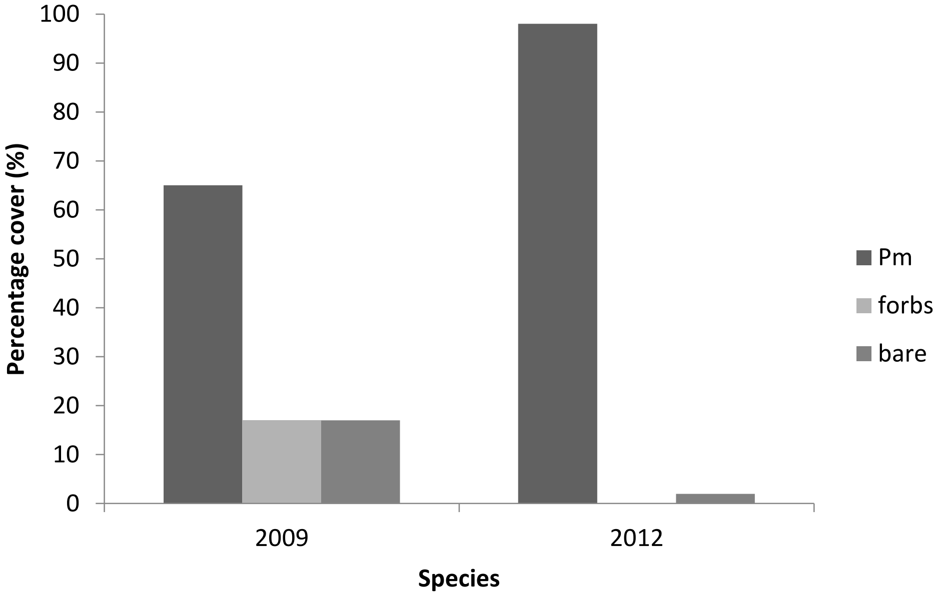

Figure 1.1: The percentage dominance of grasses, forbs and bare ground in recovering thicket areas after an extreme fire event in 2008 in HiP (Student's t-test: mean *Panicum* 2009=65%, mean *Panicum* 2012=98%, df=8, p<0.005), Where *Panicum*=*Panicum maximum*, forbs=forbs species and bare=bare ground.

This research is focused on further developing our understanding of how the medium term and landscape scale fire disturbance regime affects savanna functioning in an African mesic savanna in the context of an underlying long-term climate change disturbance regime of increased atmospheric CO_2 concentrations and temperature and possibly increased but more variable rainfall (IPCC, 2014). Furthermore, whether medium-term disturbance regimes, such as fire, can influence the direction of the potential shifts in soil nutrient, species composition and biomass driven savanna functioning by creating conditions where, (i) within the C_4 clade, species with the NADP form of C_4 photosynthesis are able to outcompete species with the PCK form of C_4 photosynthesis; and over the longer term (ii) enable C_4 species to outcompete C_3 plants. In addition, whether (iii) short-term site scale game trail barrier disturbances can impact the spread and penetration of the medium term and landscape scale fire disturbance regime, and interrupt or affect the direction of ecological interaction between these long- and medium-term processes. On this basis, to recommend management protocols for the use of fire as an effective ecological management tool.

The central questions of the thesis are related to fire spread. Grasses may differ in flammability for a variety of reasons, including the rate and extent of curing during the dry season. The next chapter is the analysis of seasonal patterns of curing in *Themeda triandra*, which dominates frequently burnt savanna, and *Panicum maximum* which burns less frequently. The next chapter deals with the key question of whether fire behaviour differs as a result of changes in grass species composition. Would a change in grass species composition, for example as a result of global change, lead to significant changes in fire spread, and therefore potentially change the fire regime of these savannas? An important applied question is whether any differences in fire behaviour between swards vary with fire season and/or with fire weather conditions on the day of burning. Lastly, the final chapter considers the effect of an animal factor on fire spread. Game trails are common in African landscapes with significant animal numbers. This chapter considers how these trails may influence fuel continuity and the spread of fire. Since trails often skirt the periphery of thicket clumps, the presence of animals may reduce fire damage to thickets facilitating their persistence, and aiding their spread, in an otherwise frequently burnt savanna landscape.

Study Area

This study was conducted in Hluhluwe-iMfolozi Park (HiP) (900 km^2; 288000 to 288260 S; 318430 to 328090 E), located in the Province of KwaZulu Natal, South Africa. The reserve is divided into Hluhluwe in the north, iMfolozi in the south connected by a corridor of state owned land in the middle. The park is characterised by hilly topography up to 540m elevation in the Hluhluwe area falling into broader river valleys at 40 m elevation in the iMfolozi area (Staver *et al.*, 2009). Rainfall is closely linked to elevation within the park (Balfour and Howison, 2002), producing a rainfall gradient from ~1000mm per annum in the higher elevations in Hluhluwe to ~600mm per annum in the lower elevations in iMfolozi (Staver *et al.,* 2009), with the rainy season peaking between October and March. The region experiences hot, wet summers and cool, dry winters; monthly mean minimum temperature is 13°C and the mean maximum temperature is 35°C (Balfour and Howison, 2001).

Most of the park is covered by *Acacia* savannas, *Euclea* thickets, and patches of *Celtis-Harpephyllum* forests (Whateley and Porter 1983). Much of Hluhluwe is covered by tall grassveld types with scattered trees and shrubs forming a mosaic with typical savanna thornveld, bushveld and thicket patches of the Zululand Lowveld vegetation unit (Mucina and Rutherford 2006). The dominant vegetation is *Acacia* savanna forming mosaics with forest and *Euclea* thicket in the northern end of the reserve. Fire is currently a major characteristic of the savanna landscape in HiP, but the fire regime varies substantially within the park (Balfour and Howison, 2001; Staver *et al.,* 2009). In general, these savannas will carry fire if sufficient fuel is left in the dry season. The mesic north end of the park is therefore the most frequently burnt.

The study area was located within the mesic *Acacia* savanna in the northern region of the park, where study plots were established on Manzibomvu hill, near Memorial Gate (figure1.2 and 1.3). The grass sward differs strikingly in species composition from the lower to mid-slopes of this hill. Soils are similar with black clay-rich surface and sub-soils. The up-slope grasslands, dominated by *Panicum maximum*, have colonised the area following a severe fire which burnt through thicket vegetation following an extreme fire event in 2003

Figure 1.2: Aerial photograph of Manzibomvu hill in HiP in the dry season. The fire plots were oriented perpendicular to the paved road with each plot stretching from the road to the upper hill slopes. The lower slopes were dominated by *Themeda triandra* (reddish brown) and upper slopes by *Panicum maximum* (white). Photo: Geoff Clinning

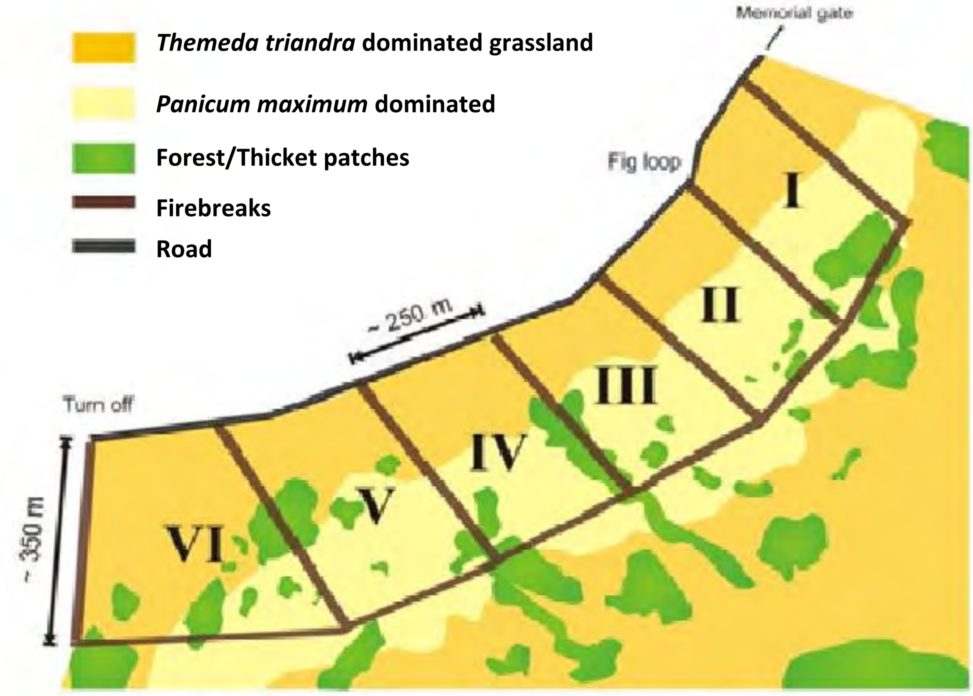

Figure 1.3: Layout of study sites on Manzibomvu hill in HiP

The grass species that were dominant in the two respective grasslands on Manzibomvu hill were *Themeda triandra* (figure 1.4, left) and *Panicum maximum* (figure 1.4, right).

Figure 1.4: *Themeda triandra* (left) and *Panicum maximum* (right)

Chapter 2: Grass species composition and phenology

Introduction

This chapter focuses on the fuel properties of grass species in two contrasting swards. The two grassland types had different predominant grass species contributing to fuel, namely, *Themeda triandra* (*Themeda*) in the more open grassland savanna and *Panicum maximum* (*Panicum*)in the recovering thicket area (Table 2.1).

It is necessary to consider the ecological dynamics observed in the Manzibomvu Hill study area in the context of the observed long-term changes to the vegetation in Hluhluwe-iMfolozi Park (HiP). Historically, the HiP was predominantly open savanna in the 1930s, but has substantially changed since then to savanna thornveld, bushveld and thicket patches (Whateley and Porter 1983; Watson and MacDonald 1983; Wigley *et al.*, 2010). Prior to the establishment of the HiP, the park was subject to a human driven fire regime ignited by cattle herders who traditionally burnt the open savanna in the late dry season to produce a green flush to support their herds at the most fodder-stressed time of the season (Balfour and Howison, 2002). This historical fire disturbance regime changed significantly after the 1895 promulgation of the HiP as park managers at the time were focussed on a veterinary tsetse fly control programme (Brooks and MacDonald, 1983) and implemented a strict fire control policy. The only fires that were supposed to have occurred were largely those ignited through natural causes, such as lightning. It was only in 1952 that a prescribed burning programme was introduced as a management practice to counter the observed phenomena of rampant bush encroachment and thicket expansion that began to become a trend in the park by that time (Brooks and MacDonald, 1983, Balfour and Howison, 2001). From the mid-1960s, burning frequency was determined to a large extent by the available fuel load, with some consideration for maintaining reserve grazing for herbivores, and this approach has continued largely unchanged till today (Balfour and Howison, 2002). In the mid-1980s, the fire management approach changed from the strict application of a block burning strategy toward an approach where fire was used to maintain or create structural and temporal patchiness in the vegetation through point source ignition and broadening the season of ignition (Balfour and Howison, 2002). This was in an attempt to promote and create patches with a range of fire histories, potentially promoting biodiversity in the landscape (Balfour and Howison, 2002). It is instructive to note that major changes in the structure and composition of the vegetation in the HiP have taken place simultaneously with changes to two long-term and large scale underlying ecological drivers. Firstly, the previously abundant population of African Elephant became locally extinct in the 1850's, due to ivory hunting pressure (Balfour and Howison, 2002). This removed elephant mega-herbivore impacts on vegetation in the region, particularly those related to woody species biomass reduction, until their re-introduction to the park in 1980. Secondly, the park has experienced an increase in atmospheric CO_2 concentration from <300 ppm at its inception to ~400 ppm in 2014 largely as a result of the industrial revolution and the burning of fossil fuels. Both direct effects on plant growth and indirect effects on climate change will have influenced vegetation change over its 120 year existence. Direct CO_2 effects are likely to be particularly important in savannas since low CO_2 is thought to account for the dominance of C_4 grasses in savannas with their competitive advantage over C_3 grasses declining at high CO_2 (e.g. Ehleringer *et al.* 1997; Collatz *et al* 1998; Sage 2004).With regards to the woody component, high CO_2 is expected to promote woody plants by enhancing their ability to recover from fire, herbivory and drought. This may have significant impacts on the structure, composition and functioning of these ecosystems even if disturbance regimes remained constant over the period (Bond, 2008; Chamaille-Jammes and Bond, 2010; Kgope *et al.* 2010; Buitenwerf *et al.* 2012; Bond and Midgley, 2012; Quirk *et al.* 2013).

In 1937 the whole of the Manzibomvu Hill study area was an open sparsely wooded savanna, except for narrow bands of closed canopy woody vegetation (thicket) along three drainage lines (Henkel, 1937, figure 2.1).The extensive closed thicket that existed on the upper reaches of the Manzibomvu Hill study area prior to the 2008 firestorm event had developed since that time. It is postulated that the development of closed thickets was as a result of changes to the disturbance regimes in northern parts of Hluhluwe, including absence of elephants for several decades, less severe fires and/or the effects of increased atmospheric CO_2 concentration on woody plants (Wrigley et al. 2010). There have been no directional trends in rainfall and temperature for this region over the last half century when woody invasion was most prominent (Bond *et al.*, 2005).

As the trees mature they also began to shade out the NADP C_4 *Themeda* dominated grassland creating conditions of low photorespiration that favour PCK C_4 species, C_3 forb and woody species and potentially C_3 grasses towards the end of the century. Thus thicket expansion into savannas perpetuates conditions of insufficient fuel loads and relatively higher moisture contents that inhibit the ability of the herbaceous layer under the canopy of the thicket to carry fire. Furthermore, dense thicket and forest reduce wind speeds in the understorey which greatly reduces rates of fire spread (e.g. Hoffmann *et al*. 2012; Little *et al*. 2012)

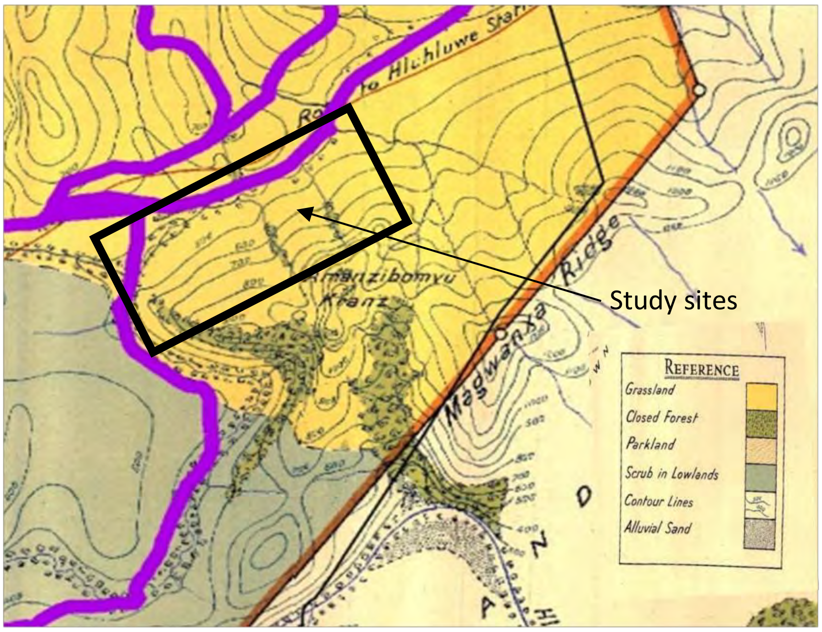

Figure 2.1: recorded vegetation types at Manzibomvu hill in HiP in 1937 from Henkel (1937)

From a fire perspective, fuel amount and moisture content are major contributors to fire spread. Different grass clades appear to differ in productivity and moisture content with Andropogoneae (*Themeda*) being highly productive but drying out early after exposure to drought compared to Paniceae (*Panicum*). In my study area, the switch from *Themeda* to *Panicum* upslope is a legacy of thicket invasion of the site, a firestorm removing the thicket, and the rapid recruitment of the burnt thicket area by *Panicum* and other panicoids and chloridoids. The switch from Andropogneae with NAPD photosynthesis to progressively less efficient photosynthetic types (e.g. PCK for *Panicum*) and eventually potentially C_3 grasses is predicted with increasing CO_2 from photosynthetic considerations (Collatz *et al*. 1998, Ehleringer and Monson 1993).

Methods

In order to explore the effect of differences in species composition, fuel curing and fuel load biomass on fire behaviour six plots were established on Manzibomvu hill in HiP using the road at the base of the hill as the start point. Each plot was approximately 250 meters wide and extended 350 meters up the hill, covering between 8 to 9 hectares. In terms of a visual assessment of vegetation type, particularly grass species composition, each plot was predominated by open savannah *Themeda* dominated grassland at the base of the hill and *Panicum* dominated grassland higher up on the hill colonising recovering thicket (see figure 1.2). Each plot was divided into two sub-plots, one consisting of the apparent *Themeda* dominated grassland at the base of the hill and the other the apparent *Panicum* dominated grassland higher up on the hill. In each individual plot, two line transects were located with GPS coordinates and grass biomass (fuel load) was estimated using disc pasture meter (DPM) measurements (Bransby and Tainton, 1977) every ten meters along the transect, totalling thirty five DPM measurements per transect (figure 2.2). At each DPM reading point, the three dominant grass species present under the disc were identified to gauge the grass species composition in each plot. Grass biomass was estimated from the DPM measurements (cm) calibrated to measured biomass at sites within HiP (R^2=0.73, N=1745) (Waldram *et al.*, 2008), as follows:

$$Grass\ Biomass\ \ \frac{g}{m^2}\ = 12.6 + 26.1\ DPM\ measurement$$

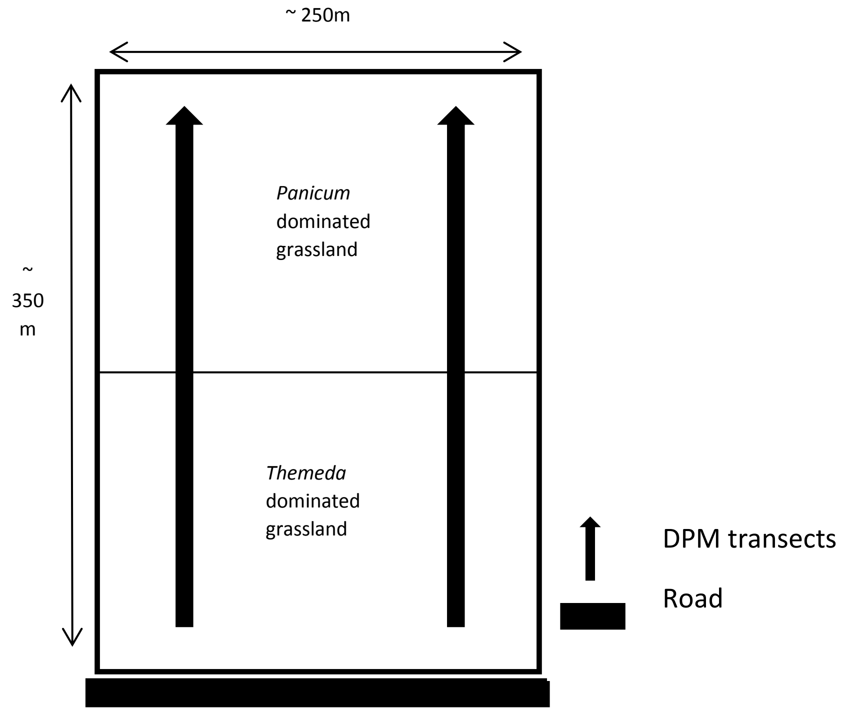

Figure 2.2: Dimensions and transect layout in a single experimental plot from the Manzibomvu hill study area. Where DPM = Disc pasture meter measurements

Grass curing is a key parameter for monitoring fire behaviour and estimating Fire Danger Indices (FDI's), as it is based on measurement or estimation of the moisture content of the fuel and because fuel moisture has a highly significant effect on the combustibility of grass fuels and the resultant fire intensity (Brown and Davis, 1973). Grass curing is defined as the proportion of dead grass fuel relative to live grass fuel expressed as a percentage (Trollope *et al.*, 2010). Differences in the fuel moisture content between *Panicum* dominated grassland and open savanna *Themeda* dominated grassland through the dry season were measured to enable the calculation of curing rate. Five sites in the northern region of Hip were identified within both the *Panicum* dominated grassland and the open savanna *Themeda* dominated grassland. At each site, ten samples of each of the dominant grass species were clipped from the grass sward every two weeks through the dry season (from 8th April to the 13th August 2013 and from 8th April to the 30th July 2014). Wet weight of each sample was recorded before the dry weight was obtained by drying the samples in a dry oven at 80°C for twenty four hours. The moisture content of each sample was then calculated by subtracting the dry weight from wet weight of the grass, as follows

$$FMC\ \% = \frac{wet\ weight - dryweight}{dry\ weight} \times 100$$

Where, FMC is fuel moisture content percentage.

Grass curing was estimated using the Trollope *et al.*, (2010) equation:

$$Grass\ Curing\ \% = 108 - (0.78\ x\ FMC\%)$$

It is useful to describe the proportion of dead grass fuel to live grass fuel when monitoring fire behaviour. However, moisture contents in this form generally vary from <10% for fully cured grass fuel to >100% for green, uncured grass fuel, which can be conceptually confusing for fire management purposes. The grass curing procedure allows one to express grass curing on a scale of 0-100% (Trollope *et al.*, 2010).

Since fuel moisture content and fuel load may be influenced by rainfall and humidity, this weather data was obtained from the South African Weather Services (SAWS) for the 2013 and 2014 seasons. The data is from the closest weather station available, based in Charters Creek some 20km from of the study area in Hip, as the research station in the park does not record the full range of weather data.

I analysed whether the grass species composition in each plot was dominated by the apparent species observed on the hill, *Panicum* and *Themeda*. I then considered two important predictors for fire intensity, the differences between grass biomass (fuel loads) and the differences between the rates of curing between *Themeda* and *Panicum.* The data were analysed using Statistical 10 and R i386 3.1.0.The differences in biomass (fuel load) of each species were examined using a Students t-test. The differences between grass curing of *Panicum* and *Themeda* in each site were examined using a Student's t test. Possible factors that affect grass curing of *Panicum* and *Themeda* through the dry season (Time of season, wind speed, humidity, rainfall and temperature) were investigated using a general linear model (GLM) (R Core development team, 2007; Crawley M.J., 2007).

Results

In order to quantify the difference in grass sward species composition between the *Themeda* dominated and *Panicum* dominated sub-plots, the DPM Percentage dominance recorded for the two species is outlined in table 2.1, which clearly shows that the sub-plots that were apparently *Themeda* dominated and *Panicum* dominated were in fact dominated by those respective species.

There was no change in percentage dominance of *Themeda* between years (Table 2.1) where *Themeda* was recorded as dominant in 90% of the *Themeda* dominated sub-plots for both years, while *Panicum* was recorded as dominant in over 76% and 73% of the *Panicum* dominated sub-plots in 2013 and 2014 respectively. In the *Panicum* dominated grasslands, Figure 2.3 indicates that other common species were present and while *Panicum* was indeed the dominant species in these sub-plots its percentage dominance appeared to have declined from 2013 to 2014. However, the difference was not significant (N=6, Z=0.63, p=0.5).

Table 2.1: Percentage species composition in each plot dominated by either *Themeda triandr*a or *Panicum maximum* in 2013 and 2014

Plot	**Percentage (%) *Themeda triandra* in 2013**	**Percentage (%) *Themeda triandra* in 2014**	**Percentage (%) *Panicum maximum* in 2013**	**Percentage (%) *Panicum maximum* in 2014**
1	97	88	68	62
2	85	84	75	74
3	97	94	81	68
4	83	84	92	71
5	100	93	74	90
6	77	94	68	74
Average	**90**	**90**	**76**	**73**

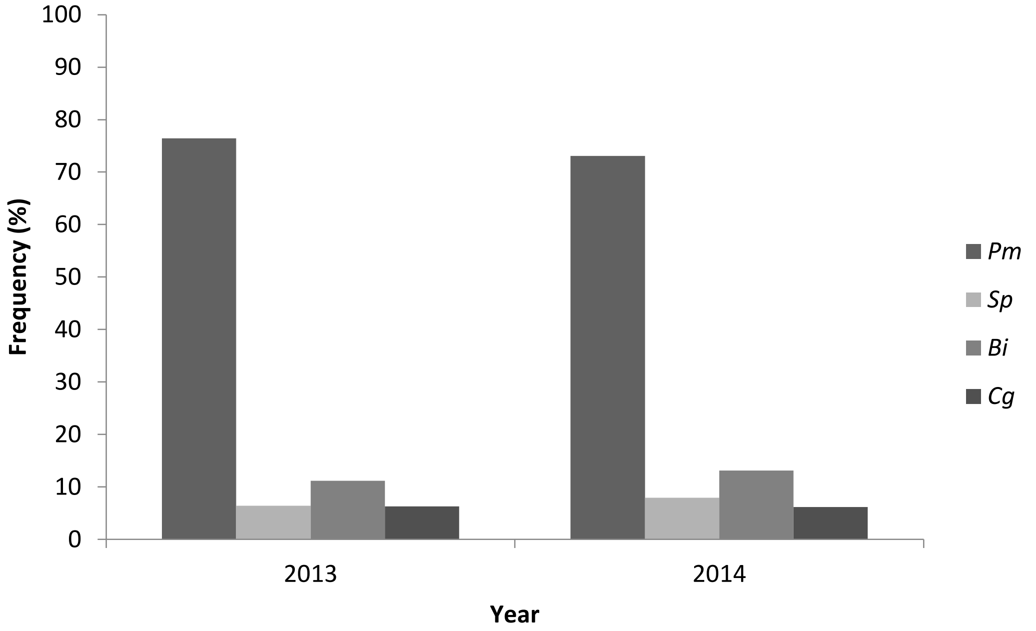

Figure 2.3: the frequency (%) of the dominant species in the *Panicum maximum* grass sward for 2013 and 2014 of 70 DPM measurements per plot, thus 840 DPM measurements over the two years. Where *Panicum*= *Panicum maximum*, *Sp* = *Sporobolus pyramidalis*, *Bi* = *Bothriochloa insculpta*, *Cg* = *Chloris gayana*

Themeda had significantly more biomass than *Panicum* (Figure 2.4) (*Themeda* in 2013, mean *Themeda*=6596 kg/ha, standard error=249 kg/ha, *Panicum* in 2013, mean *Panicum*=3650 kg/ha, standard error=298 kg/ha, df=10, p<0.001) (*Themeda* in 2014, mean *Themeda*=5425 kg/ha, standard error=671 kg/ha, *Panicum* in 2014, mean *Panicum*=3226 kg/ha, standard error=257 kg/ha, df=10, p<0.001).

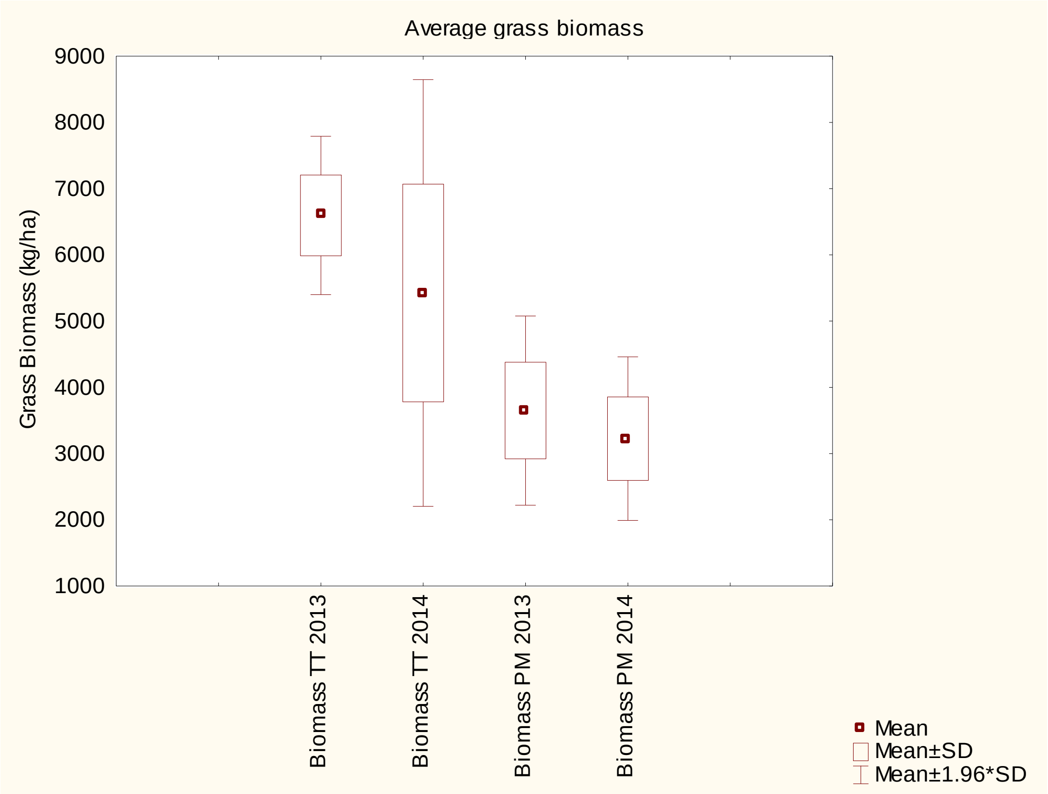

Figure 2.4: the average grass biomass present in all of the plots dominated by *Themeda triandra* or *Panicum maximum* for 2013 and 2014

Figure 2.5 and 2.6 outline the percentage curing trends for both *Panicum* and *Themeda* grasslands during each of the 2013 and 2014 dry seasons, respectively. There was a significant difference in curing between *Panicum* and *Themeda* in both years. The curing in 2013 (mean *Panicum*=79%, standard error= 2.3%, mean *Themeda*=89%, standard error= 1.6%, df =14, p=0.002) (figure 2.5) and the curing in 2014 (mean *Panicum*=77%, standard error= 2.6%, mean *Themeda*=87%, standard error= 1.8%, df=14, p=0.007) (figure 2.6). In both 2013 and 2014, *Themeda* began both dry seasons significantly more cured (at over 80%) than *Panicum* (at some 60% in 2013 and 70% in 2014). Further, *Themeda* cured more rapidly than *Panicum* throughout the dry season, with *Themeda* being dryer than *Panicum* at the end of the dry season.

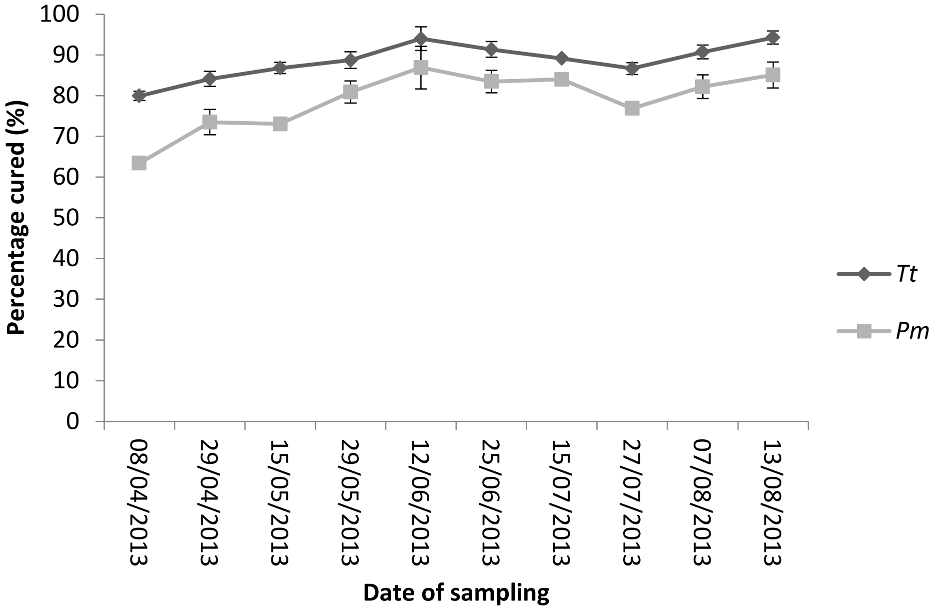

Figure 2.5: the percentage grass curing from April to August of *Themeda triandra* (*Tt*) and *Panicum maximum* (*Pm*) in 2014, (+SE)

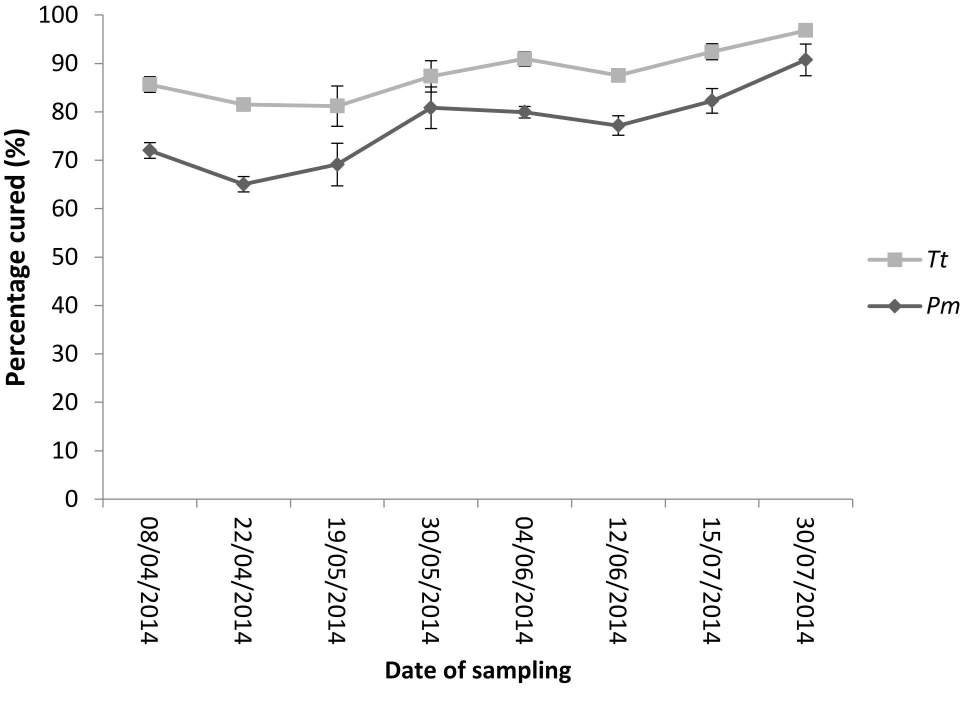

Figure 2.6: the percentage grass curing from April to July of *Themeda triandra* (*Tt*) and *Panicum maximum* (*Pm*) in 2014, (+SE)

The degree of curing in *Panicum* was affected by season, while season had no effect on *Themeda* (Table 2.2).

Table 2.2: A general linear model for the grass curing of *Panicum maximum* and *Themeda triandra* in 2013 and 2014. The weather data is for the two year period obtained from SAWS

Explanatory variables that contribute to grass curing	**Time in the fire season**	**Wind speed (kph)**	**Humidity (%)**	**Temperature (°C)**	**Rainfall (mm)**
Panicum maximum					
Coefficient estimate	0.014	-0.02	-0.0008	0.01	-0.001
Degrees of freedom	16	12	13	14	15
SE	0.005	0.09	0.005	0.03	0.002
z	2.8	-0.23	-0.15	0.41	-0.44
P	**0.006**	0.8	0.9	0.7	0.7
Themeda triandra					
Coefficient estimate	0.008	-0.03	-0.001	0.01	-0.0003
Degrees of freedom	16	13	15	14	12
SE	0.005	0.08	0.005	0.03	0.002
z	1.6	-0.33	-0.26	0.4	-0.12
P	0.1	0.7	0.8	0.7	0.9

Discussion

The fire regime in savannas has been shown to be a significant determinant of the vegetation species composition and structure, and therefore a major ecological driver of the functioning of these ecosystems (Bond and Van Wilgen 1996; Anderson, Cook and Williams 2003, Higgins *et al,* 2007; van Wilgen *et al,* 2007). Regular fires are important to maintain the functioning of open savanna grasslands as fire affects the balance of tree and grass recruitment prevents grass moribidity and increases woody species mortality (Govender *et* *al.*, 2006). The factors that affect fire behaviour in grasslands are grass biomass (fuel load), fuel moisture content and the weather conditions on the day of the burn. Grass biomass is an important contributing factor to fire intensity (Govender *et al.,* 2006) because fire spread is linked to grassy fuel loads (Hennenberg *et al.*, 2006). The most important influence of fuel moisture on fire behaviour is the smothering effect of the water vapour released from the burning fuel. There is more heat energy being used in evaporating the water from the grasses than there is being used for combustion, thus creating a lower rate of combustion (Brown and Davis, 1973; Tainton, 1999). The moisture content of the grass sward varies considerably as a result of seasonal curing, and this in turn has a significant effect on fire intensity (Govender *et al.*, 2006; Leonard, 2009).

The Manzibomvu Hill study area comprises open savanna grassland at the bottom of the hill, dominated by *Themeda* and further up on the hill, grassland dominated by *Panicum* in areas that were burnt thicket (Table 2.1, see figure 1.2 and 1.3). However, once a firestorm opened up the closed canopy in the recovering thicket areas, the *Panicum* dominated grass layer had developed fuel loads of up to 4000 kg/ha and above, therefore meeting the requirement of sufficient fuel to carry a fire through its grass layer (Trollope et al., 2002). Furthermore, this study area in the northern part of HiP has been subjected to frequent fires over the last six years, specifically beginning with the fire storm of 2008 a biennial frequency up to 2012 (2008, 2010 and 2012) and from then, an annual frequency up to 2014 (2012, 2013 and 2014).

In this context, it is hypothesised that the Manzibomvu Hill open savanna *Themeda* dominated grassland would exhibit fire adapted features and therefore be in a stable state under the high frequency fire regime. The *Themeda* dominated grassland had almost double the amount of biomass (fuel load) than that of the *Panicum* dominated grassland in both 2013 and 2014 (figure 2.4). Further, *Themeda* dominated grassland cured at a significantly faster rate and to a higher level than the *Panicum* dominated grassland and key variables expected to affect curing, such as time of season, temperature, wind, humidity and rainfall had no significant effect at all. In fact, *Themeda* was already over 80% cured at the start of both dry seasons, whereas *Panicum* began the dry seasons at approximately 60% cured in 2013 and 70% cured in 2014 (Figures 2.5 and 2.6). Further, the open savanna *Themeda* dominated grassland showed no change in species composition over several years (Table 2.1) suggesting that this grassland is fire adapted and in a stable state under a high frequency fire regime.

Although there was no significant difference between percentage dominance of *Panicum* between 2013 and 2014, figure 2.3 shows a higher richness of the grass species composition in the recovering thicket by 2013 and 2014, with contributions from other species (*Sporobolus pyramidalis, Bothriochloa insculpta* and *Chloris gayana*) to the grass layer, which were not recorded earlier in the six year high fire frequency period in adjacent recovering thicket areas in the northern part of Hip by Browne (2009) or Wills (2012) (Figure 1.1). In this context, it is postulated that if the high frequency fire disturbance regime were to continue over the medium-term, the impacts of fire would continue to reduce any remaining canopy cover and deplete the soil nutrient status in the recovering thicket area by draining below ground biomass reserves through the regular removal of above ground biomass. Overtime, this may create the conditions that enable a succession of species with the more efficient NADP form of C_4 photosynthesis to establish and out-compete species with a PCK form of C_4 photosynthesis. This would likely lead to the increasing dominance of fire adapted species typical of the more open savanna in the recovering thicket area. Changing species composition over time, may gradually transform the fuel characteristics of the recovering thicket grassland to those observed in the *Themeda* dominated grassland, which in turn, creates fuel conditions favouring the perpetuation of a high frequency and more intense fire disturbance regime.

However, since *Panicum* and *Themeda* cure at different rates (figure 2.5 and 2.6), Table 2.2 shows that time of burn in the season is a significant factor affecting the fuel curing (moisture content) of the *Panicum* dominated grassland and would be an important factor affecting fire behaviour in these areas. This suggests the need to burn later in the season in *Panicum* dominated grasslands or on a very hot and dry day to achieve similar fire intensity obtained in open savanna grasslands such as those dominated by *Themeda*.

Conversely, if grass species composition changes due to changing climate, especially increasing atmospheric CO_2 concentrations and in the absence of a suitable medium-term fire disturbance regime we may see a reversal in the shift in species composition in the recovering thicket areas. Besides increasing recruitment of C_3 woody species re-establishing an increasingly closed canopy cover (e.g. Wigley *et al*., 2010) high CO_2 is likely to lead to an increase in PCK species within the C_4 grass clade and eventually possibly an outright shift to C_3 grass species towards the end of the century (Collatz *et* al., 1988; Chamaille-Jammes and Bond, 2010). The next chapter explores the consequence of a change in grass species composition on fire behaviour in this study area.

Chapter 3: Grass species composition and fire behaviour

Introduction

Tree and grass recruitment and tree mortality in savannas are significantly affected by fire intensity (Govender *et al.*, 2006) and fire may be the dominant factor driving observed shifts between grassland and closed woodland habitats in savannas (Bond *et al.*, 2005). This effect of fire is especially strong in mesic savannas with more than 650 mm of rain annually (Sankaran *et al.*, 2005). In this chapter, fire properties are compared between the open *Themeda* dominated savanna grassland and the *Panicum* dominated grassland of recovering thicket in the mesic savanna of Hluhluwe discussed in Chapter 2. This Chapter examines the effect of timing of fire in the dry season and fire weather on the day of burn on fire intensity, and completeness of burn, within the respective grasslands. I compared the results of experimental burns with simulations from fire behaviour models to determine whether the models are sufficiently accurate to enable them to be used as fire management decision support tools.

Over the last century, mesic savannas in Hluhluwe have been colonised by closed woody thicket vegetation causing major changes in plant and animal life in areas affected (Wigley *et al.*, 2010; Parr *et al.*, 2012). However, since the new millennium, several high intensity fires, ‘fire storms’ have occurred. Unlike the usual fires which do not burn beyond the margins of the thicket, fire storms burn deep into thicket patches and have also burnt 100s of meters into tall scrap forest (Browne, 2009; Browne and Bond, 2011). Fire storms provide an opportunity for reclaiming savanna. It is postulated that once a closed thicket has initially been opened up, a high frequency fire regime, implemented over the medium-term can, favour a switch to a grassland state and, eventually, to the fire adapted open savanna stable state that existed historically. Conversely, in the absence of a high frequency fire regime, the successional post-burn process could lead to recovery of the closed thicket state. Given this conceptual framework, the following questions arise:

Firstly, can the timing of the fire in the dry season in savannas be adjusted to influence fire intensity so as to promote a grassland state? If restoring savannas were the objective for the recovering grassland, then complete, frequent and high intensity burns would be required to promote typical open grassland savanna. Experience in savannas generally suggests that late season burns would be most effective for this purpose (Trapnell, 1959; Andersen *et al*. 2003; Laris and Wardell, 2006; Furley *et al*., 2008). In contrast, early season burns would be preferred if the objective were to allow the recovery of burnt densely wooded savanna or thicket.

Secondly, can similar desired fire intensity and burn completeness effects be achieved using the fire weather of the day irrespective of the time in the fire season? This is based on the assumption that higher fire danger days result in increased fire intensity and completeness of burn.

Thirdly, can fire behaviour models predict fire intensity in grasslands dominated by *Themeda* and *Panicum* respectively and therefore be useful as decision support tools in ecological management through the use of fire?

Methods

Experimental fires:

Fire breaks were cut and burned around each of the 6 plots referred to in Chapter 2 to enable the application of experimental fire treatments.

In order to examine the effects of the time of burn in the fire season and the effect of fire weather three experimental fire treatments were conducted in the plots, at different times in the fire season; ‘early’ season (at the beginning of the dry season, i.e. end of June) and ‘late’ season (towards the end of the dry season, i.e. mid-August) fires, as well as, fires conducted on a “red day”. A “red day” refers to a day where it is considered too dangerous to burn according to the fire danger index (FDI) and consists of conditions of more than 30°C, less than 30% humidity and wind speeds exceeding 20kph (Trollope and Trollope, 2007). This Fire Danger Rating system was adapted by Winston Trollope from the system developed by Stewart Meikel and Johan and Lizette Heine from the Forest Fire Association in Nelspruit, South Africa. In each treatment, four replicate burns were conducted. Each of the fires burned through the respective subplots of *Themeda triandra* (*Themeda*) and *Panicum maximum* (*Panicum*) dominated grass layers. Before each fire, moisture content data was collected using the same method outlined in Chapter 2. The FDI was calculated on each fire day to ensure that the weather conditions within each of the ‘early’ season or ‘late’ season fire treatments were similar. Further, the FDI was calculated on the day of the “red day” burns and recorded.

Using a drip torch, back fires were first put in at the top (highest elevation) of each plot followed immediately by setting the head fire from the lowest elevation. The ignition pattern was then completed with drip lines around the perimeter of the plot. The start time of the fires were recorded for both *Themeda* and *Panicum* subplots. Six 3.5 meter poles were put in a straight line at forty meter intervals following the direction of the wind for each sub-plot per plot (figure 3.1) and thus were in line with the direction of the fire front. This ensured that each subplot of *Themeda* and *Panicum* had 3 poles. The exact time that the fire front reached each pole was recorded. Then the end time of the fire was recorded for both *Themeda* and *Panicum* subplots as well as the overall burn time. During the course of each fire, fire weather conditions (i.e. temperature, humidity, wind speed and wind direction) were monitored and recorded every ten minutes using a Kestrel 3000 Pocket Weather Meter.

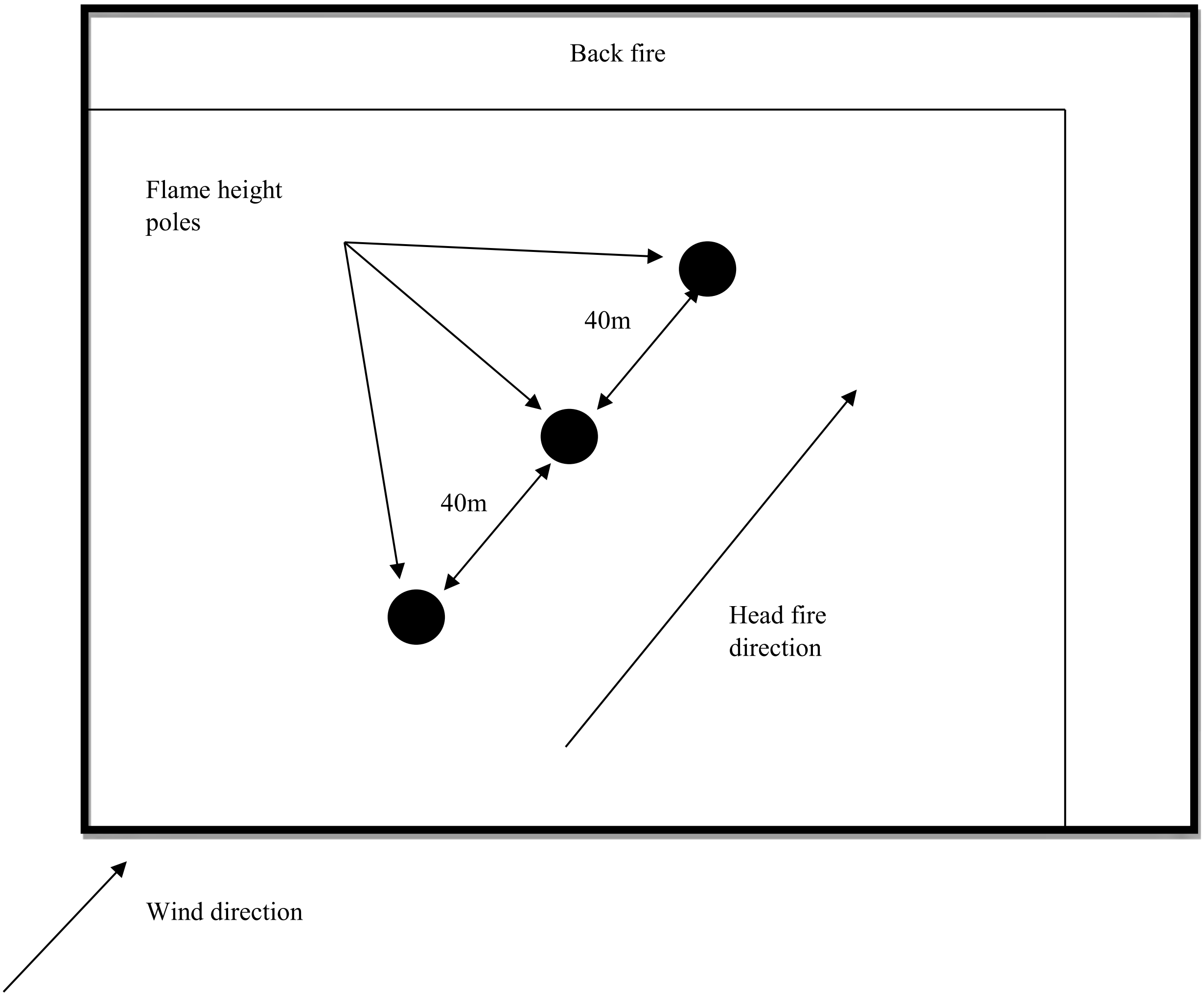

Figure 3.1: the fire protocol for igniting fires in each subplot of *Themeda* and *Panicum* per plot at different times in the fire season

Rate of fire spread was calculated from the time it took for the fire to reach each pole. Flame height was recorded at each sub-plot dominated by the respective grass species by measuring the highest point on the poles where string attached at 25cm intervals on each pole had burnt off. Fire intensity was calculated using rate of spread and biomass of grass fuel with Byram's fire intensity equation (Byram, 1959, Trollope et al., 2002):

$$I = H \; x \; w \; x \; r$$

Where I = fire intensity (kJ/s/m), H = heat yield (kJ/kg) (16890 kJ/kg), w = mass of available fuel (kg/m^2), r = rate of spread of the fire front (m/s), (kJ/s/m = kW/m).

Fire Models:

In order to test whether fire behaviour models could be used as effective fire management decision tools, two fire behaviour models were used to simulate fire behaviour for a typical savanna in Hluhluwe-iMfolozi Park (HiP) and compared against the observed fire intensities obtained in the experimental fires. The two models used were the BehavePLus5 model (Hoffman *et al.*, 2012) and the fire intensity model from Trollope and Trollope (2002).

The BehavePlus5 model is based on Rothermel's (1972) fire spread equations, and predicts fire behaviour for a user-defined set of fuel and environmental conditions (Hoffman *et al.*, 2012). The model was parameterized to simulate four fuel moisture content scenarios to differentiate the moisture content of the two grass species and as a proxy for 'early', 'late' and 'red day' fire season conditions. The four scenarios included: for the 'early' season fires *Themeda* moisture was classified as 1/3 cured and *Panicum* was classified as fully green; for 'late' season and 'red day' fires *Themeda* was classified as fully cured and *Panicum* was classified as 2/3 cured. The model required information on fuel loads which were obtained from the DPM readings that differentiate the two grass species (see Chapter 2). The model also required information on the proportion of fuel that was living or dead, which was obtained from measured values in typical mesic savannas in HiP (van Wilgen and Wills, 1988).

The Trollope and Trollope (2002) fire intensity model is an empirically derived equation describing the relationship between fire intensity and key driver variables, namely fuel load, fuel moisture, relative humidity and wind speed as follows:

$$FI = 2729 + 0.8684\, x_1 - 530\, \sqrt{x_2} - 0.907\, x_3^2 - 5961/x_4$$

Where FI = fire intensity (kJ/s/m), x_1 = fuel load (kg/ha), x_2 = fuel moisture (%), x_3 = relative humidity (%), x_4 = wind speed (m/s).

The observed values for *Themeda* and *Panicum* fuel status and fire weather were inserted into the model to predict the respective fire intensities for each grass sward type.

Possible factors that affect fire intensity in all fires ignited in 2013 and 2014 (Biomass, fuel moisture, wind speed, temperature, relative humidity and slope) were investigated using a general linear model (GLM) (R Core development team, 2007; Crawley M.J., 2007).The GLM was poisson and the terms were fitted according to their assumed importance, i.e. fire intensity is likely determined by biomass, fuel moisture content and weather on the day of the fire. I analysed the factors contributing to variation in fire intensity across the entire data set to explore the main predictor variables. I then analysed the factors contributing to fire intensity separately for *Themeda triandra* (*Themeda*) and *Panicum maximum* (*Panicum*). I was particularly interested to determine whether differences between *Themeda* and *Panicum* burns was related to differences in fuel loads between the species or whether intrinsic species properties, including curing rates, also produced different responses. I then compared the predicted fire intensities from the two fire models against the observed fire intensity, in order to gauge the predictive power of the respective fire intensity models. The data were analysed using Statistica 10, Microsoft Excel and R i386 3.1.0. A Student's t-test was used to test the difference in fire intensity between *Themeda* and *Panicum* and to test the difference between rates of fire spread and grass biomass for *Themeda* and *Panicum*. An Anova was used to test the difference in fire intensity of *Themeda* between fire seasons and whether there was a significant difference in fire intensity for *Panicum* between fire seasons. A least squares regression was used to explore the relationship between relative humidity on the day of the fire and fire intensity in grass swards dominated by *Panicum*. A regression analysis was used to test whether the fire behaviour models predict similar patterns of fire intensity to those observed in the experimental fire treatments.

Results

The 12 fires that were ignited over two years were all allowed to burn to completion through the respective grass swards. The fire weather data on the day of the fires, the dates and times of the fires are in Appendix 1. The summary for the fire behaviour variables are presented in Appendix 2.

Contributions to fire intensity:

The GLM (table 3.1) analysis indicates that the differences in fire behaviour observed across all fires at different times could be attributed to the difference in grass species composition (i.e. *Themeda* and *Panicum* dominated grass swards) the timing of the fires in the season and the fuel loads.

Table 3.1: general linear model for factors contributing to the differences in fire intensity of grass swards across different times in the fires season for all fires

Explanatory variables that contribute to fire intensity	**Treatment (Early season, Late season, Red day)**	**Species effect (*Themeda* or *Panicum*)**	**Biomass (kg/ha)**	**Fuel moisture (%)**	**Temperature (°C)**	**Wind speed (kph))**	**Relative humidity (%)**	**Slope (%)**
Coefficient estimate	0.03	0.05	0.000	0.02	-0.003	0.0009	-0.003	-0.002
Degrees of freedom	19	19	19	17	18	13	15	14
SE	0.009	0.02	0.000006	0.003	0.003	0.002	0.004	0.004
t	3.5	2.6	1.3	0.9	-0.9	0.4	-0.7	-0.4
p	**0.003**	**0.02**	0.1	0.4	0.4	0.7	0.5	0.7

Figure 3.2 indicates that there are differences in fire intensity between *Themeda* and *Panicum* for all fires, with *Themeda* swards experiencing significantly higher fire intensities that *Panicum* swards (Mean fire intensity in *Themeda* swards = 5024 kW/m, standard error = 828 kW/m, mean fire intensity in *Panicum* swards = 1686 kW/m, standard error = 250 kW/m, df = 21, $p<0.001$). Figure 3.3 displays a similar pattern and suggests that the flame heights detected this pattern of differing fire intensities between the two species.

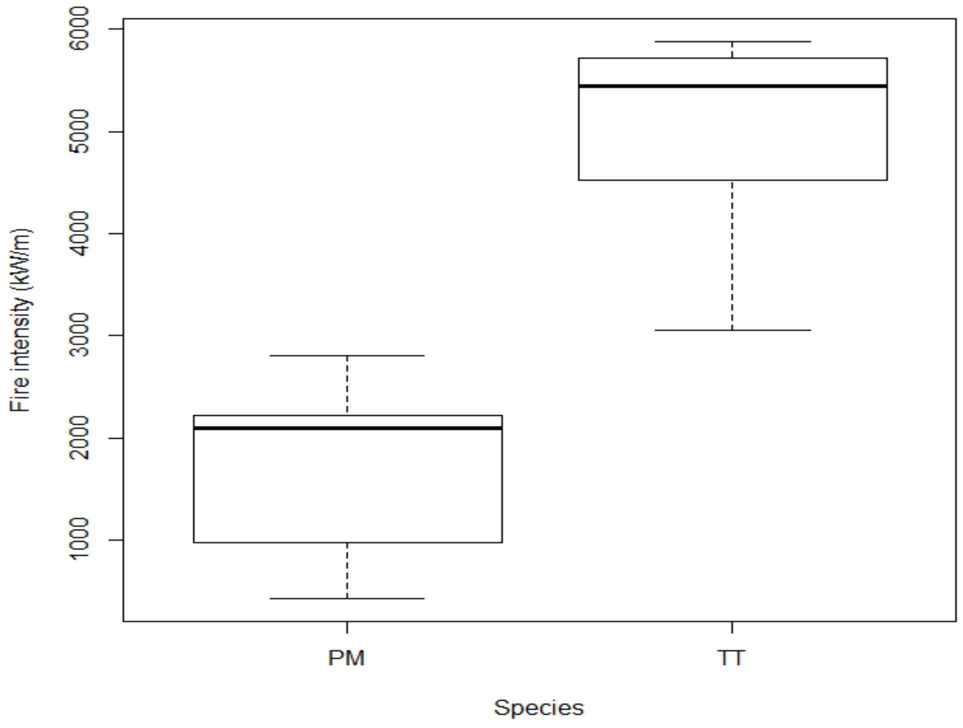

Figure 3.2: the difference in fire intensity of all fires of *Themeda triandra* (*Themeda*) and *Panicum maximum* (*Panicum*) for 2013 and 2014. Where TT=*Themeda* and PM=*Panicum*

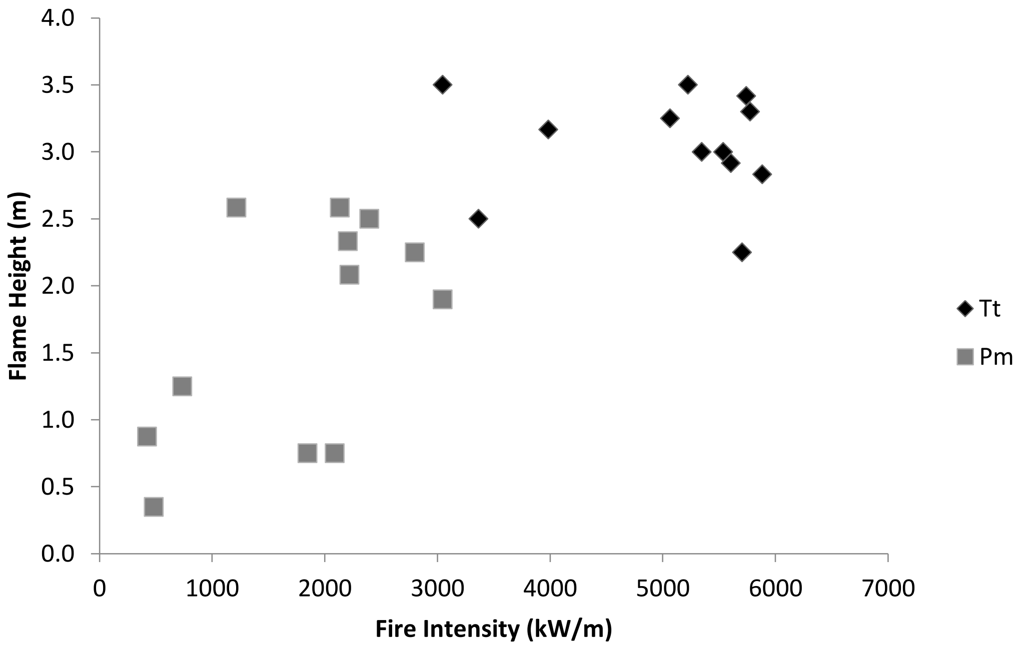

Figure 3.3: The average fire intensities experienced in Themeda triandra swards and Panicum maximum swards compared to the flame heights observed at different times in the fire season for 2013 and 2014. Where Tt= *Themeda* and PM= *Panicum*

Figure 3.4 shows that *Themeda* swards burnt more readily and more intensely in both 2013 and 2014 than *Panicum* swards did. There were significant differences in the fire intensity in grass swards dominated by *Themeda* versus *Panicum* for all three experimental fire treatments ('early' season burn (mean *Themeda*=4193 kW/m, standard error = 878 kW/m, mean *Panicum*=856 kW/m, standard error = 315 kW/m, df=6, p=0.01), 'late' season burn (mean *Themeda*=6053 kW/m, standard error = 571 kW/m, mean *Panicum*=2134 kW/m, standard error = 115 kW/m, df=6, p<0.01) and 'red day' burn (mean *Themeda*=4528 kW/m, standard error = 513 kW/m, mean *Panicum*=3097 kW/m, standard error = 203 kW/m, df=6, p=0.04)). There was no significant difference in fire intensity recorded for the *Themeda* dominated grassland fires between 'early' season, 'late' season or 'red day' burns, whereas, fire intensities in *Panicum* dominated grass swards differed significantly between the different burn treatments (Figure 3.4). *Themeda* differs in fire intensities between seasons, with the early season fire experiencing the lowest fire intensity and the late season fire experiencing the highest fire intensity. However, there was no significant difference (F=2.17, df=2, p>0.05) found between the three burn times, i.e. early season, late season and red day. The variation could be due to a difference in the fuel loads between these three fires. In contrast, *Panicum* dominated grasslands experienced significant differences (F=24.7, df =2, p<0.01) in fire intensities between burns at different times in the season. The fire intensity increased with each burn time in the fire season, with the highest intensity occurring during the red day and perhaps importantly, this was also a late season fire.

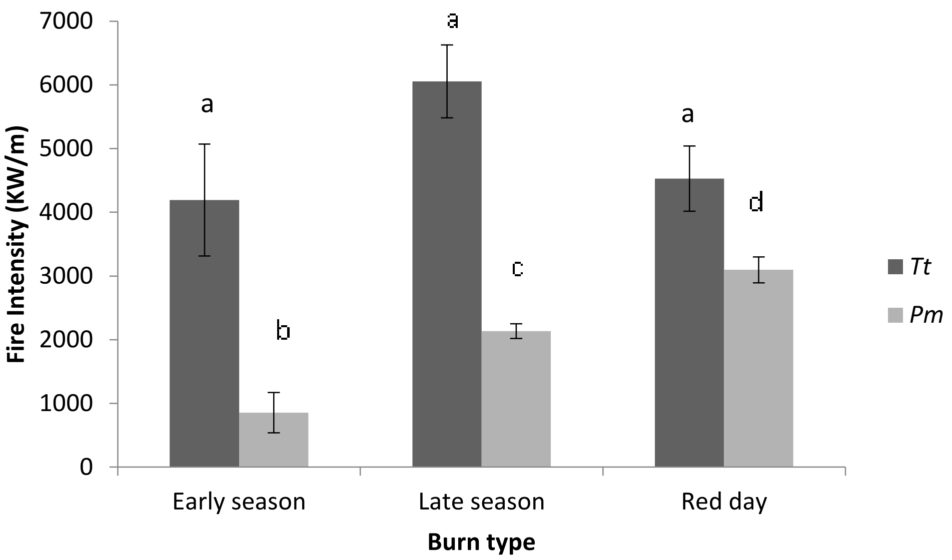

Figure 3.4: The average fire intensity recorded per experimental fire treatment for *Themeda triandra* (*Themeda*) dominated grasslands and *Panicum maximum* (*Panicum*) dominated grasslands during the fire seasons in 2013 and 2014. Bars show average fire intensity (+SE). The letters above each bar denote significant difference. Where Tt= *Themeda* and PM= *Panicum*

Contributors to fire intensity of Themeda triandra and of Panicum maximum:

Table 3.2 considers the factors contributing to the differences in fire behaviour within the *Panicum* swards and the *Themeda* swards. The GLM (table 3.2) suggests that the most important factor that influenced fire intensity in *Panicum* dominated grasslands is overwhelmingly the time of season. Relative humidity on the day of the fire has a lesser influence as well. For *Themeda* dominated grass swards, biomass seemed to be the overwhelming factor influencing the fire intensity of these fires.

Table 3.2: general linear model for the factors affecting the variation in fire behaviour for *Themeda triandra* swards and *Panicum maximum* swards across the different times in the season for 2013 and 2014

Explanatory variables that contribute to grass curing	**Treatment (Early season, Late season, Red day)**	**Biomass (kg/ha)**	**Fuel moisture (%)**	**Temperature (°C)**	**Wind speed (kph))**	**Relative humidity (%)**	**Slope (%)**
Panicum maximum							
Coefficient estimate	0.66	0.00005	-0.04	-0.04	0.02	8.7	-0.05
Degrees of freedom	9	6	8	5	6	7	5
SE	0.11	0.005	0.04	0.2	0.02	2.9	0.04
t	6.1	-0.4	-1.1	-0.2	1.1	3	-1
p	**0.0002**	0.7	0.3	0.8	0.3	**0.02**	0.4
Themeda triandra							
Coefficient estimate	-0.003	0.00003	-0.009	-0.005	0.002	-0.006	-0.004
Degrees of freedom	7	9	8	7	6	4	5
SE	0.01	0.000007	0.006	0.004	0.004	0.005	0.003
t	-0.2	4.3	-1.7	-1.3	-1.6	-1.2	-1.2
p	0.8	**0.002**	0.1	0.2	0.3	0.3	0.1

Figure 3.5 suggested that biomass is important for fire behaviour in *Themeda* grass swards (R^2=0.65, n=11, df =10, p<0.01). However, the biomass effect seemed to steady, suggesting that once biomass accumulates over approximately 5500 kg/ha – 6000kg/ha, the spread of the fires did not increase as much.

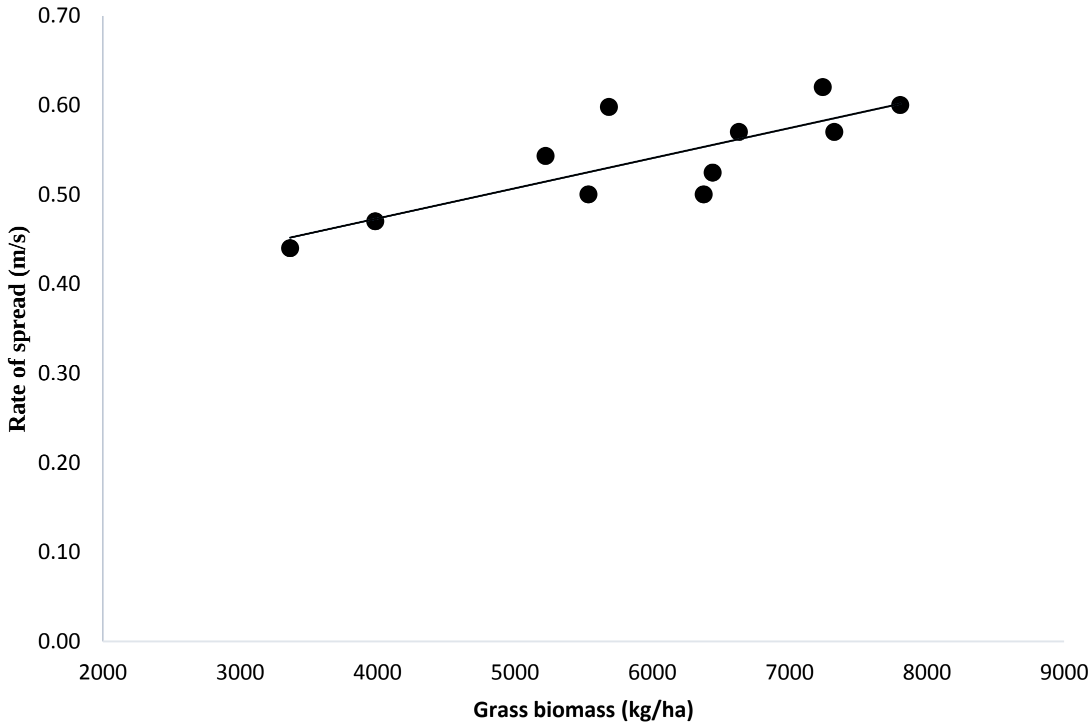

Figure 3.5: The relationship between rates of spread and fuel biomass for *Themeda triandra* dominated grasslands. The equation for the graph is $y = 3e^{-0.5x} + 0.3388$

Panicum grass swards experienced more intense burns when the relative humidity on the day was low (figure 3.6) (n=11, df =10, p<0.001). *Panicum* dominated grasslands had lower biomass than *Themeda* dominated grasslands overall (see Chapter 2), but biomass only had a little effect on the rate of spread experienced during the *Panicum* dominated grasslands experimental fires. *Panicum* dominated grasslands generally experienced high rates of spread when there was higher fuel loads (figure 3.7). However, the effect of season on the rate of spread in *Panicum* dominated grasslands are perhaps more important than biomass.

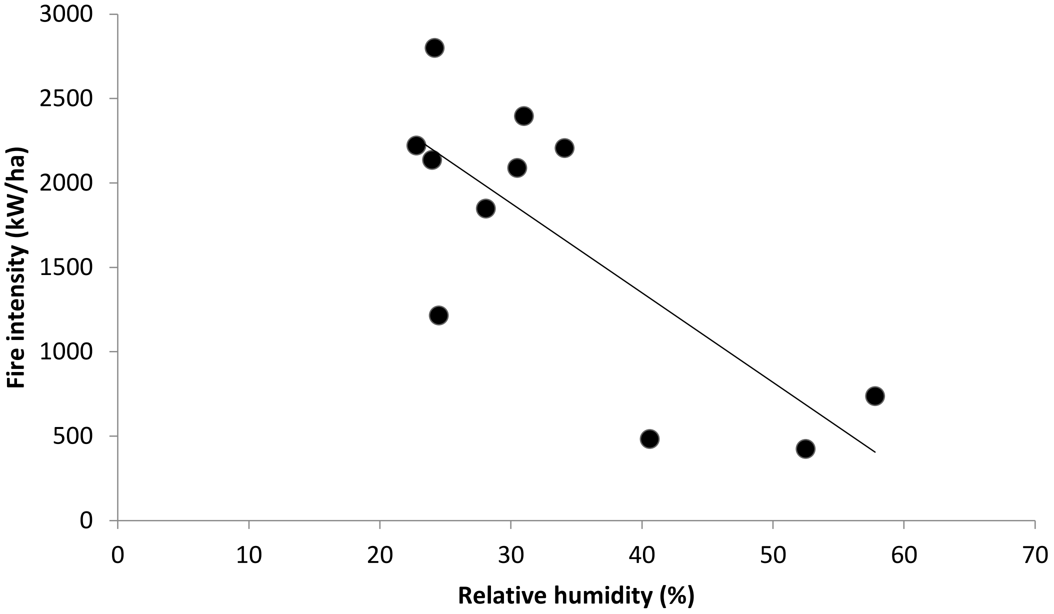

Figure 3.6: Regression analysis of the relationship between relative humidity and fire intensity for *Panicum maximum* dominated grasslands. The equation is y = -53x + 3470, R^2=0.58

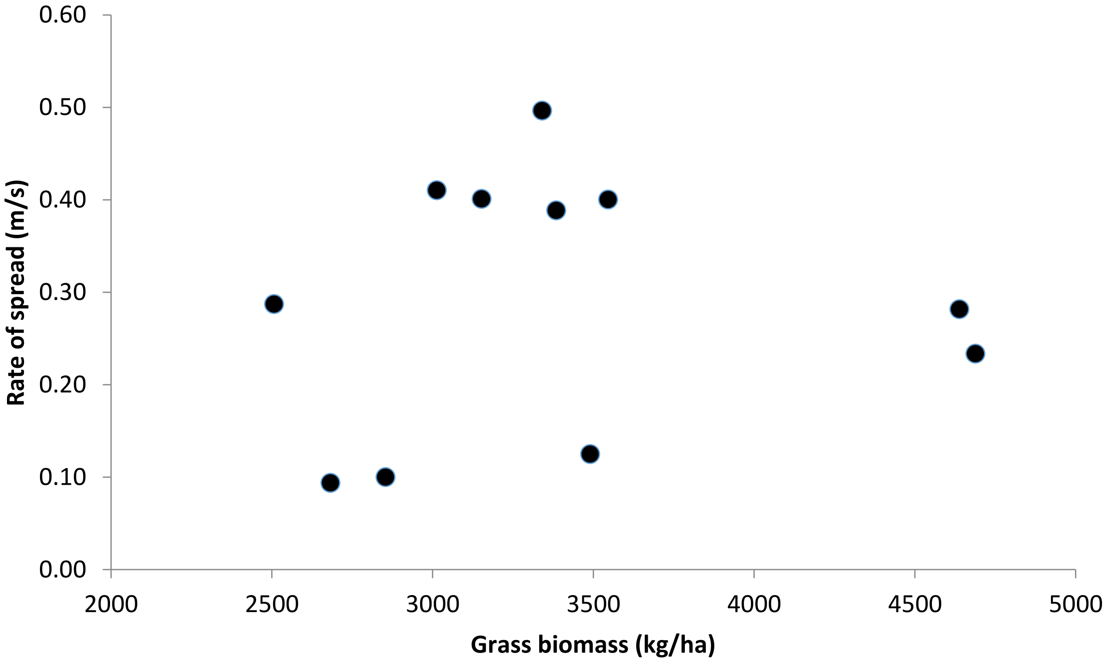

Figure3.7: the relationship between rates of spread and fuel biomass for *Panicum maximum* dominated grasslands for each site

Fire intensity models:

The fire behaviour parameters and variables are presented in Appendix 3 and Appendix 4.

Both models predicted that *Themeda* dominated grasslands had a higher fire intensity than *Panicum* dominated grasslands, although the models under estimate the intensities slightly. This difference in fire intensities between *Themeda* dominated grasslands and *Panicum* dominated grasslands observed from both models suggests that the main driver variables are the difference in fuel load and fuel moisture, as the two grass species differed significantly in these two factors (Table 3.3). The Trollope and Trollope fire intensity model (figure 3.8) predicted the intensities fairly well (R^2=0.68, p<0.001) at lower fire intensity, however, the model under-predicted observed values as the fire intensities increased. The BehavePlus5 fire behaviour model (figure 3.9) predicted the fire intensities more effectively (R^2=0.75, p<0.001), although, it over-predicted at higher fire intensities.

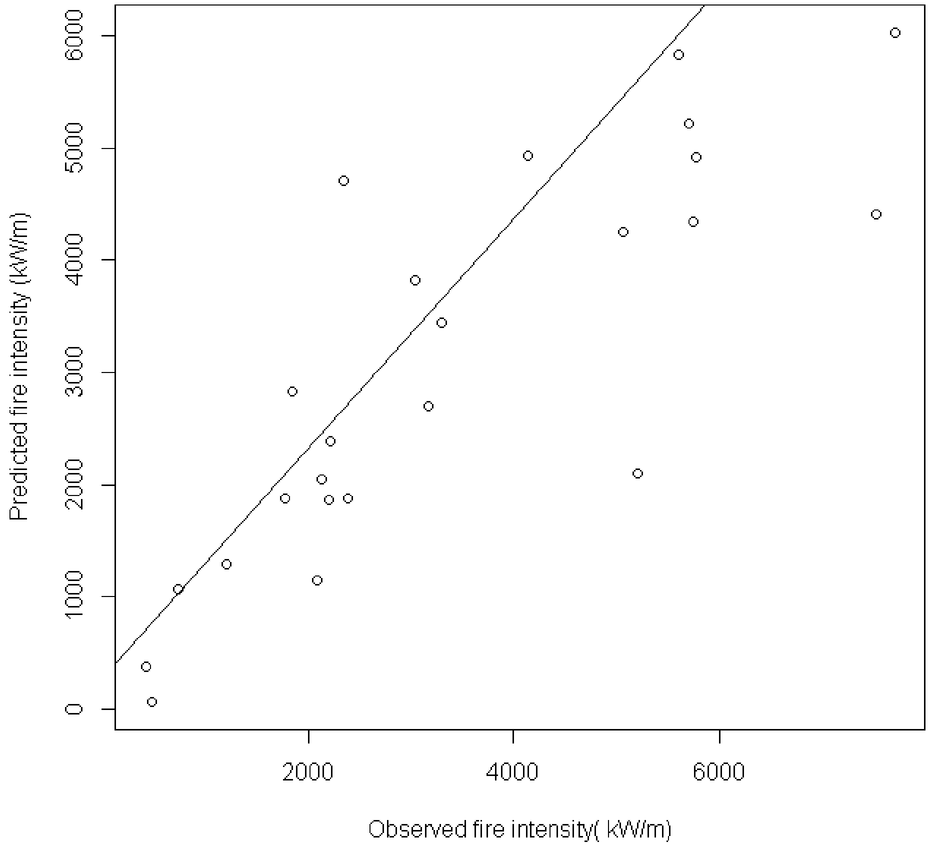

Figure 3.8: Analysis showing the observed fire intensities against the predicted fire intensities from the Trollope and Trollope (2002) fire intensity model

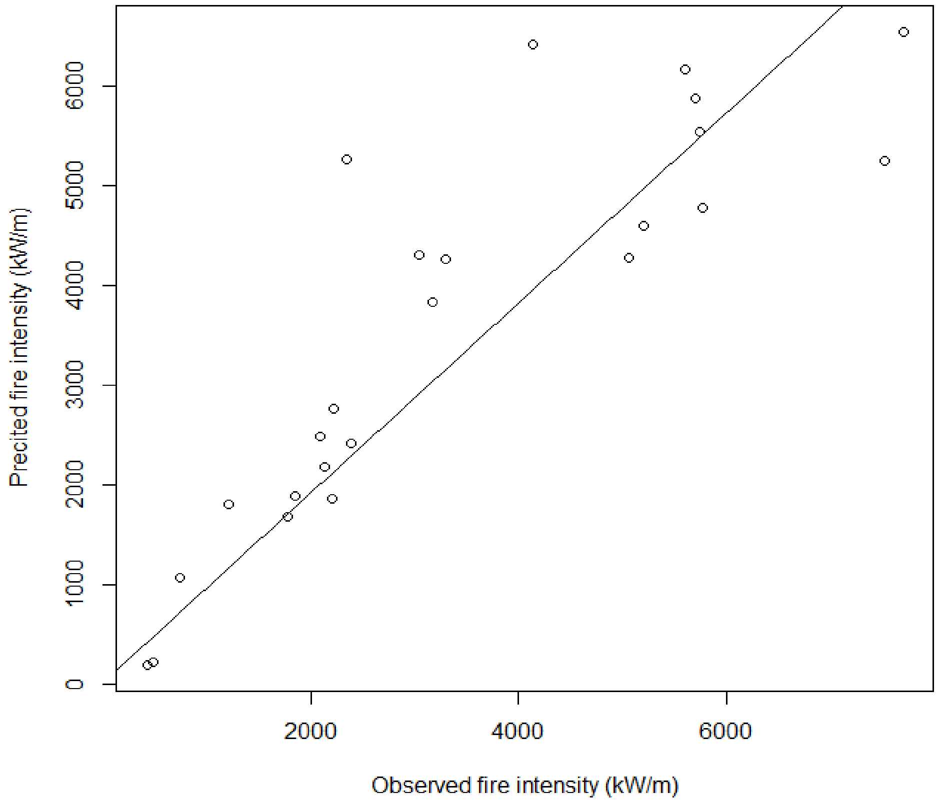

Figure 3.9: Analysis showing the observed fire intensities against the predicted fire intensities from the BehavePlus5 fire behaviour model

Table 3.3: a comparison of the fire intensity for the BehavePlus5 model and the Trollope and Trollope model against the observed values obtained from the experimental fires

Source	***Themeda triandra***			***Panicum maximum***		
	Fuel loads (kg/ha)	**Moisture content (%)**	**Fire Intensity (kW/m)**	**Fuel loads (kg/ha)**	**Moisture content (%)**	**Fire Intensity (kW/m)**
This Study	3364-7807	16-25	3047-7702	2507-4288	28-45	424-5200
BehavePlus5 model predictions	3364-7807	16-25	3836-6543	2507-4288	28-45	195-4599
Trollope and Trollope model predictions	3364-7807	16-25	2702-6030	2507-4288	28-45	64-2825

Discussion

Fire is an important ecological driver in savanna ecosystems. There are a range of species with different physiological and anatomical adaptations present in these ecosystems. They are all affected by fire and perhaps influence fire behaviour in their own right due to differences in their fuel characteristics. In this study, open savanna and recovering thicket grass swards dominated by *Themeda triandra* (*Themeda*) and *Panicum maximum* (*Panicum*) respectively, burnt differently under the same fire weather conditions. This supports the conclusion that changes in grass composition with different fuel characteristics would therefore impact the fire regime in Hluhluwe-iMfolozi Park (HiP).

The context of this study was to determine how grass species composition influences fire behaviour in an African mesic savanna. This may be influential for fire management to either promote savannas or promote closed woody vegetation (thickets). Importantly, grass species flammability potentially differs, which is being suggested by Ripley *et al.,* (2010). Even on the account of the biomass differences between the respective grass species, *Themeda* swards burns more fiercely than *Panicum* swards. Chapter 2 suggests that this difference in fire intensity may be due to curing, as suggested by the change in fire behaviour through the season for *Panicum.* Therefore, grass species composition is important for which fire regime is used for which management objective. Thus, the questions are can the timing of igniting fires be used to achieve higher intensity fires? Does fire weather on the day of the fire compensate for fire season? Finally, can fire behaviour models simulate fire reasonably accurately, so that they may be used as fire management tools?

Overall, the fire behaviour on Manzibomvu hill was influenced by grassy fuel loads present at the time of the fire (table 3.1). The grass species composition was an influential factor that contributed to the differences in fire behaviour in the study site (table 3.1). The differences observed in the fire intensities of the fire may be attributed to the differences in the dominant grass species contributing to fuel load in the area that is being burned, namely, *Themeda* and *Panicum* dominated grass swards. The *Themeda* dominated grass swards generated higher intensity fires in 2013 and 2014 than the grass swards dominated by *Panicum* (figure 3.2, figure 3.3). This suggests that these species differ greatly in their fuel characteristics.

The differences in fire intensity are more pronounced earlier on in the fire season, which may be due to the differences in the curing rates between the two dominant species. *Themeda* cures more rapidly than *Panicum* does and has significantly lower moisture content throughout the season than that of *Panicum* (see Chapter 2). Therefore, as observed, *Themeda* dominated grasslands burn more readily than *Panicum* dominated grasslands do. The fuel loads between the two grasslands differ, with *Themeda* dominated grasslands having a significantly higher fuel load than grasslands dominated by *Panicum*. These factors may contribute to the higher rates of spread seen in the open savanna *Themeda* dominated grassland fires. The type, amount, and moisture content of the fuel load are strongly related to fire behaviour, especially fire intensity and rate of spread (Whelan 1995).

The fuel loads and fire intensities reported here are similar with those reported for other savanna regions in Africa and those of the early season fires in northern Australian savannas (Table 3.4). However the extreme fire weather conditions observed in the late season fires, as well as differences in fuel composition in Australia, are the likely factors that generate the higher fire intensities observed in the Australian late season fires and the Kruger National Park high intensity fires (Williams, Gill and Moore, 2003, Govender *et al.*, 2006).

Table 3.4: Comparative fuel load and fire intensity data from savanna vegetation in Africa and Australia

Place	**Number of fires**	**Fuel loads (kg/ha)**	**Fire-line intensity (kW/m)**	**Source**
Kruger national park	956	830-9214	28-17905	Govender *et al.,* (2006)
Hluhluwe-iMfolozi park	10	1600-5964	194-5993	Van Wilgen and Wills, (1998)
Early season fires, Northern Territory, Australia	15	2100–6000	500–3100	Williams, Gill and Moore, (2003)
Late season fires, Northern Territory, Australia Ecology,	10	3000-9800	3700-18000	Williams, Gill and Moore, (2003)
Hluhluwe-iMfolozi park	12	2507-7807	424-7702	This Study

It is evident that fire intensity differs between the grass swards. *Themeda* dominated grasslands experience higher fire intensities than grasslands dominated by *Panicum*. However, when looking at a large sward of grasses in a savanna, this difference may not be as clear. There may be variation in fire intensity within the same fire, especially if the area is large (Govender et al., 2006). This raises the question of which factors are most important for managing fire intensity and therefore the completeness of burn? For the experimental fires conducted in HiP, there were variations in the fire intensities and this was likely due to the different factors affecting fire behaviour in the two grasslands. For the most part, the GLM analysis indicated that fire weather (i.e. temperature, wind speed and relative humidity) at the time of the fires seemed less important for fire intensity. The variables that were more pronounced as important factors affecting fire intensity in the *Panicum* dominated grasslands were time of season and relative humidity on the day of the burn (table 3.2). Fire season was an overwhelmingly important factor driving fire intensity in *Panicum* dominated grasslands, as time of season is related to curing of the grass (see Chapter 2). On the other hand, biomass (fuel load) was the most important in explaining the variation in fire intensity seen in grasslands dominated by *Themeda* (table 3.2). It is important to note, that the other variables, such as slope and fire weather are still important factors when considering fire behaviour in grasslands at a landscape scale.

As suggested by the GLM analysis, fire season is less important for *Themeda* dominated grasslands. This may be attributed to the curing characteristics of the species seen in Chapter 2, as *Themeda* begins the dry season already cured to a high level and dries out quickly through the season and therefore is able to burn readily at any time in the fire season (figure 3.4). Although the difference between the late season burn and the red day burn were not significant in the open savanna grassland, the apparently lower fire intensity experienced on the red day seems to be linked to fuel load. There was a higher fuel load of *Themeda* present for the late season burns than there was for the red day burns (see Chapter 2). This suggests that high fuel loads are important for achieving high rates of spread with *Themeda* dominated grassy fuels. The fuel load effect reaches a peak (asymptoting above ~5500 kg/ha), where increasing the fuel loads no longer increases the rates of fire spread experienced in grasslands dominated by *Themeda* (figure 3.5). This suggests that biomass only drives fire behaviour to a certain level, at which point, other factors such as slope and fire weather, could play more important roles in increasing the spread rates of the fires. This may suggest that there are thresholds for fire intensities with regard to fires that burn through open savannas, where grass is the dominant fuel type. The intensity of these fires may only increase with sufficient woody vegetation, where the fire reaches sufficient intensity to switch from a surface fire to a canopy fire. These sets of conditions are characteristic at the edges between open savanna and closed thicket mosaic and, in this context, may have implications for managing the phenomenon of woody plant encroachment in mesic savannas.

Panicum, on the other hand, behaves differently to the typical open savanna grass species. *Panicum* tends to grow in and immediately adjacent to thicket patches, often underneath trees due to its physiological C_4 PCK photosynthetic pathway adaptation. Consequently *Panicum* has higher moisture contents than *Themeda* and thus lower levels of curing (see Chapter 2).

The GLM analysis showed that time of burn in the fire season is the most important variable explaining the increased intensity of fires in *Panicum* dominated grassy fuels (figure 3.5). Specifically in *Panicum* dominated grassland, low fire intensities were experienced in the early season and the fire intensity increased as the dry season progressed, with relatively high intensities in the late season fires and even higher intensities on the red day burns. The fuel loads were similar across seasons and fire days, suggesting that curing was the key variable accounting for intensity differences since fuel moisture content decreased from early to late in the fire season (see Chapter 2). However, the difference in fire intensity seen between the late season fires and the red day fires suggests that fire weather is also an important factor that can increase the intensity of fires in *Panicum* dominated grassy fuels. The GLM analysis suggests that relative humidity is the most critical fire weather factor driving the increase in fire intensity of fires burning through *Panicum* dominated grass swards. Therefore, the observed difference in fire intensity that *Panicum* dominated grassland experienced between the late season fires and the red day fires was likely related to the impact of fire weather. This effect may be attributed to the relatively higher moisture content of *Panicum*, which makes relative humidity on the day of the fire an important determinant. Decreasing relative humidity contributes to a higher level of fuel drying at the fire front and increase fuel flammability, driving the intensity of the fire upward (figure 3.6). This indicates that in recovering thicket areas or at the edge of closed thickets patches, burning later in the fire season and/or burning on a very hot and dry day would result in the increased intensity of fires that burn through *Panicum* dominated swards. Therefore, this may affect the completeness (spread or penetration) of the burn. In addition, biomass (fuel load) is also an important determinant of rate of spread (figure 3.7); even though its degree of importance was less pronounced in *Panicum* dominated grasslands than it was in *Themeda* dominated grassland (Table 3.2).

The fire intensity models predict that *Themeda* dominated grassland would yield more intense fires than *Panicum* dominated grassland would (table 3.3). These models are based on fuel loads (biomass) and curing levels (fuel moisture content), which are the primary differentiating factors between these grasslands (see Chapter 2).Therefore; it is unsurprising that they would generate these results. The Trollope and Trollope (2002) fire intensity model (figure 3.8) and the BehavePlus5 fire behaviour model (figure 3.9) predict the differences in fire intensity between the open savanna *Themeda* dominated grassland and the recovering thicket *Panicum* dominated grassland clearly and also perform relatively well in predicting the intensities of the fires. The Trollope and Trollope (2002) model under estimates fire intensity at its observed higher intensity levels while the BehavePlus5 model over-estimates fire intensity at these observed levels. *Themeda* dominated grassland do not seem to be heavily impacted by fire weather and fuel moisture, because it dries out quickly and burns readily. This suggests that fuel load is the more important determinant of fire intensity in these grasslands. The variable accuracy of the performance of these fire behaviour models may be due to variance in the *Panicum* based estimates of fuel load, especially in the case of the *Themeda* dominated grassland, where fuel load is much higher and a major contributing factor to fire intensity. The disc pasture meter loses accuracy at higher biomass loads (Bransby and Tainton, 1977), which may contribute to the inaccuracy of these models at the high end of their spectrums.

Chapter 4: Game trails and fire spread

Introduction

Fire and grazing are key consumers in savannas (Archibald *et al*., 2005). They have been shown to influence vegetation structure, composition, annual above ground net primary production and nutrient cycling (Archibald *et al*., 2005). Grazers could have indirect effects on modifying their habitats, by altering the fire regime (Waldram *et al.,* 2008). This may be through the creation of heavily grazed grazing lawns that act as biological barriers preventing fire spread (Waldram *et al*., 2008). This chapter considers one effect of animals that has not been previously documented, to my knowledge, for African savannas; the effect of game trails on fire spread.

Carvalho *et al.* (2011) noted that leaf-cutter ants remove leaf litter and woody debris (potential fuels for fire) in and around their nests. This led to the consideration that leaf cutter ants influence fire spread, because they remove potential fuel not only from their nests but also along their trails. The ants create trails with completely bare mineral soil, effectively creating firebreaks, which stop low-intensity fires from spreading from savannas into forest edges at the South American forest-savanna boundary (Carvalho et al., 2011). Game trails are similar trail structures present in African savannas, where large herbivores create paths in and around thicket and forest patches through hoof-action rather than by the removal of vegetation.

This chapter considered the effects of short term, site specific, small scale disturbances. Game trails are present between the open savanna and thicket patches in Hluhluwe. These game trails were generally formed around the remaining closed thicket patches and less frequently within the recovering thicket grasslands in the Manzibomvu Hill study area (figure 4.1). It is hypothesised that these game trails, which are substantially larger than those of the leaf cutter ants, would be able to act as firebreaks around thicket patches during the fires that burn through the savannas at relatively higher intensities. If the trails are able to act as barriers against fire, then thickets that have these barriers around them are more likely to be ‘protected’ from fire than those that do not have trails around them. Fire behaviour at the savanna/thicket boundary may also differ depending on the presence or absence of trail-creating mammals. Considering that the trails are variable in size; one would expect that wider trails are more likely to ‘protect’ thickets than narrower trails. Similarly, grassland fuel loads in savannas, and in a thicket patch, might be expected to influence whether fires would cross the trail and burn into the thickets. Finally, there may be differences in grass species composition in the grassland and thicket edge vegetation types, which could impact fire behaviour. This chapter reports a study of the effects of game trails on fire behaviour in the experimental fire plots set out in Hluhluwe.

Figure 4.1: an example of a game trail surrounding a thicket patch

Methods

The game trails identified on the Manzibomvu Hill study area were largely situated toward the middle of the hill at the edges of remaining closed thicket patches within the recovering thicket on the hill. A wandering quarter method was used to locate trail sites (Catana, 1963). Sites were selected based on whether there was contrasting vegetation/fuel type present, i.e. where the grassland bordered a closed thicket patch. Thirty sites, where there was a game trail present at the edges of closed thicket and grassland patches (a “trail” site) and twenty control sites, that had no game trail present at the edges of the closed thicket and grassland patches (a “no trail” site) were located. The GPS coordinates of each site were recorded, so they might be located again. In addition, sites where there was a game trail present were selected to ensure that the orientation of the trail was approximately on the contour and therefore, likely to be perpendicular to the direction of the fire treatment (figure 4.2).

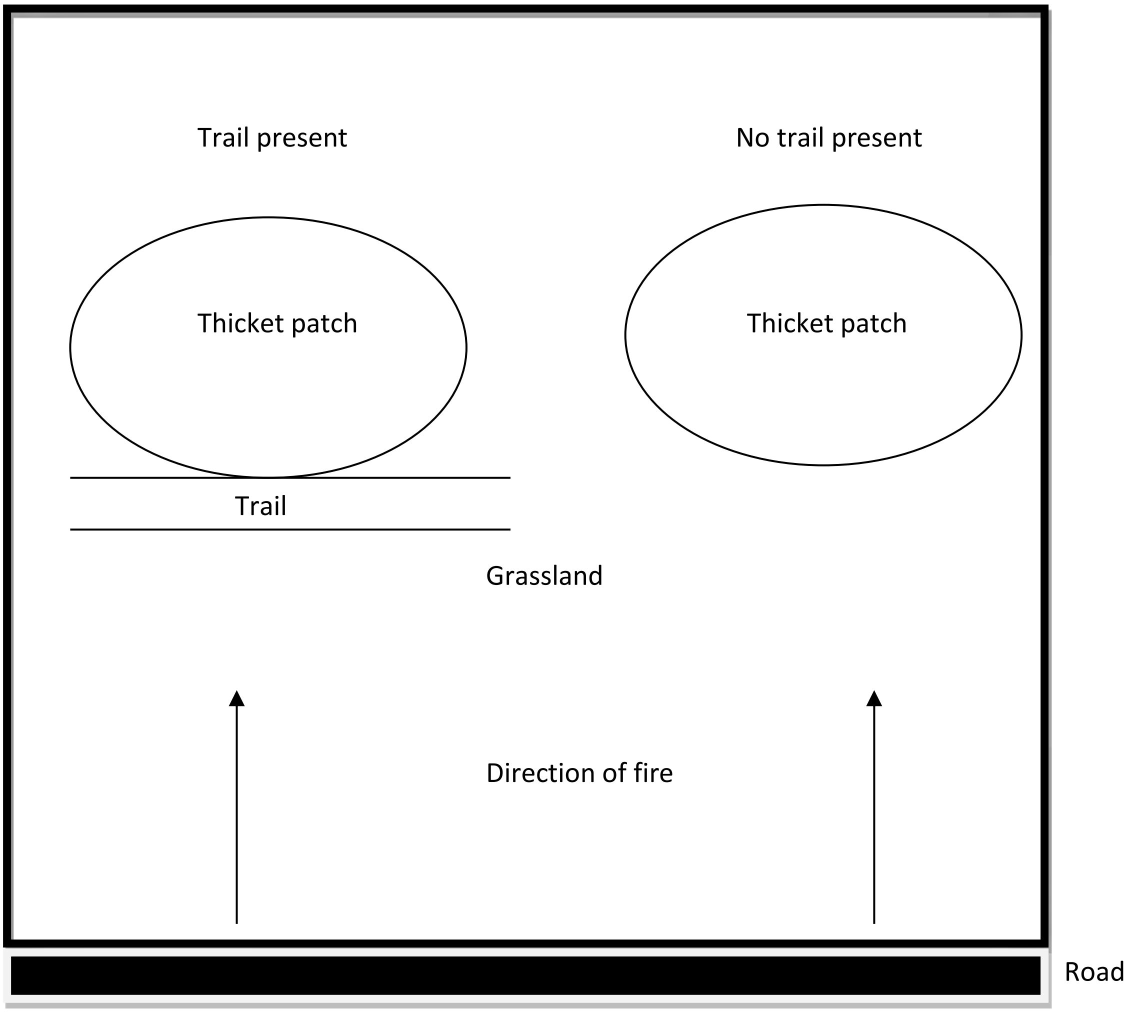

Figure 4.2: an illustration of the study sites where there was a trail present and when there was no trail present on Manzibomvu hill

At each site, grass DPM biomass measurements and the species composition beneath the disc were recorded in the grassland leading up to the thicket patch and into the thicket patches (see Chapter 2 methods). At each site six, DPM readings in the grassland and six DPM readings in the thicket patches were taken at random within a ten meter radius of the trail or border of the thicket edge.

At each “trail” site the width of the trail was measured at three different points and an average trail width calculated and a note was taken of whether the trail was either completely bare or covered over with vegetation (which consisted of grass and/or litter).

The fires that burned through the “trail” and “no trail” sites were ‘red day’ fires (see Chapter 3) to ensure that the fire weather was constant and that the fire would most likely be able to burn through each site, regardless of grass species composition. At each site six “burn severity” estimates were recorded in the grassland and six “burn severity” estimates in the thicket patches were taken at random within a ten meter radius. The “burn severity” was estimated within a 0.5 by 0.5 meter quadrat using the following categories; 0-25% burnt = did not burn; 25-69% burnt = partially burnt and 70-100% burnt = fully burnt (figure 4.3).

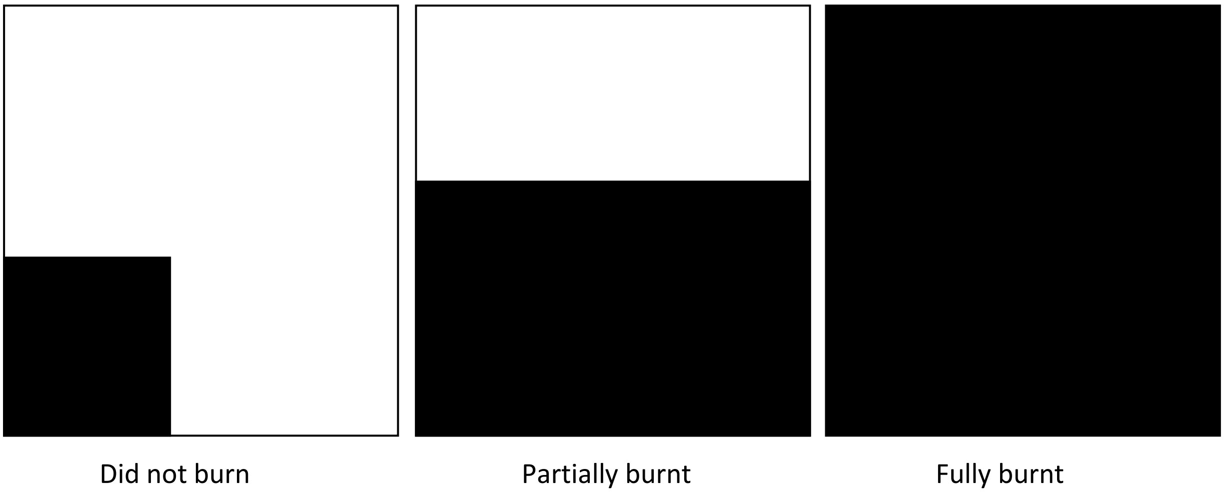

Figure 4.3: the estimates of burn severity in the quadrats for each treatment

The grass biomass and the grass species composition in the grasslands and the thickets were analysed to gauge whether fires would be able to spread through the areas. Factors contributing of whether fire would cross into thicket patches with the presence of game trails or not were analysed and the frequency of occurrence was considered. The data were analysed using Statistica 10, Microsoft Excel and R i386 3.1.0. Possible factors that may affect whether the fire carried through into the thicket areas from the grasslands (presence of a trail or not, the width of the trail and the grass biomass) were investigated using a general linear model (GLM) (R Core development team, 2007; Crawley M.J., 2007). Differences in grass biomass between the grasslands and the thicket patches at the sites where there were "trails" present and at the sites where there were "no trails" present were tested using a Student's t-test. A Chi squared test for independence was used to test the difference between trail presence or not and whether the fire burnt into the thicket patches or not.

Results

Figure 4.4 showed that there was a significant difference in the grass biomass in the grassland and the thicket patches ("Trail" sites: mean grass biomass in grassland=3703 (kg/ha), standard error= 300 kg/ha, mean grass biomass in thicket patches=1739 (kg/ha),standard error= 195 kg/ha, df=58, p<0.001; "No trail" sites: mean grass biomass in grassland=4398 (kg/ha), standard error= 387 kg/ha, mean grass biomass in thicket patches=2215 (kg/ha), standard error= 219 kg/ha, df=38, p<0.001). However, the grass biomass did not differ significantly between the "trail" and "no trail" grasslands or the "trail" and "no trail" thicket patches (p=0.16, p=0.12, respectively).

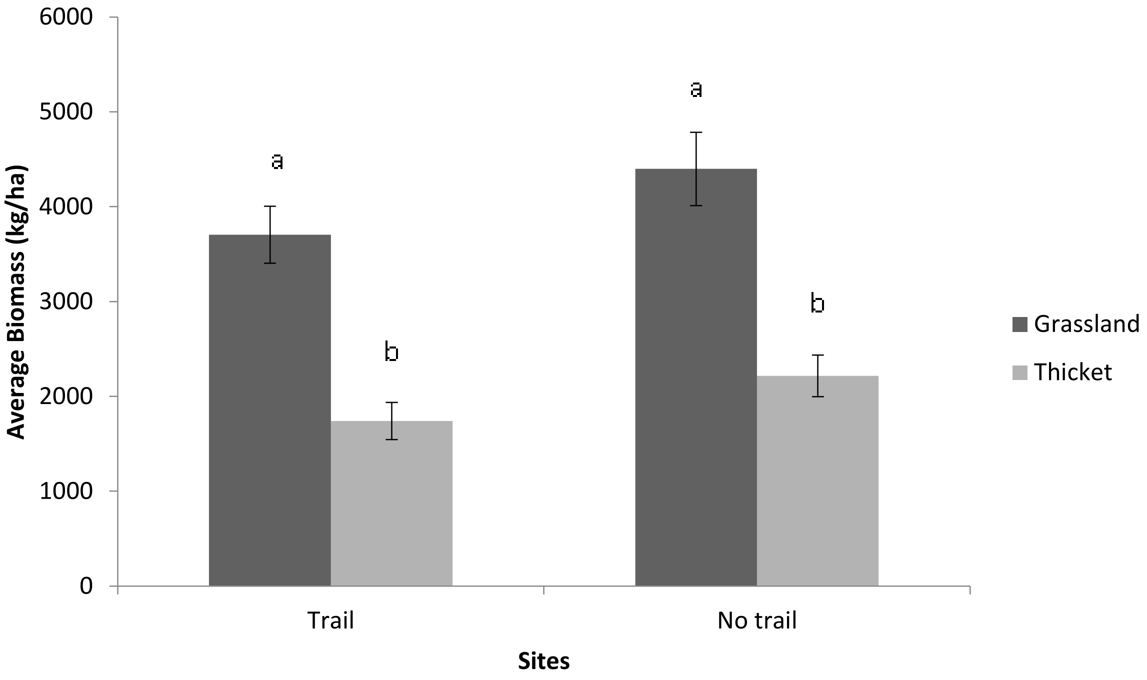

Figure 4.4: the average biomass present in the grassland leading up to the thicket and the average biomass in the ticket areas for the treatments, trail present and no trail present. The letters above the bars denote significant difference, (+SE)

Figure 4.5 indicates that the grassland areas leading up to the thicket patches were mostly dominated by *Themeda triandra* (*Themeda*) and *Panicum maximum* (*Panicum*) for the treatments, “trail” present and “no trail” present. The grass species composition in the thicket patch sites for both treatments was dominated by *Panicum* (Figure 4.6).

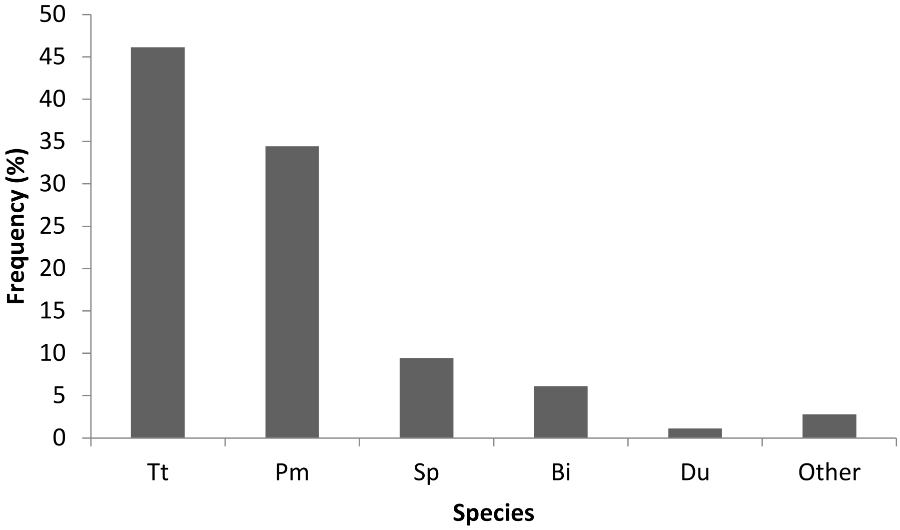

Figure 4.5: the overall grass species composition (frequency %) in the grassland leading up to the thickets for both treatments. Where *Themeda*= *Themeda triandra*, *Panicum*= *Panicum maximum*, *Sp*= *Sporobolus pyramidalis*, *Bi*= *Bothriochloa insculpta*, *Du*= *Dactyloctenium australe*, Other= Bare ground and forbs

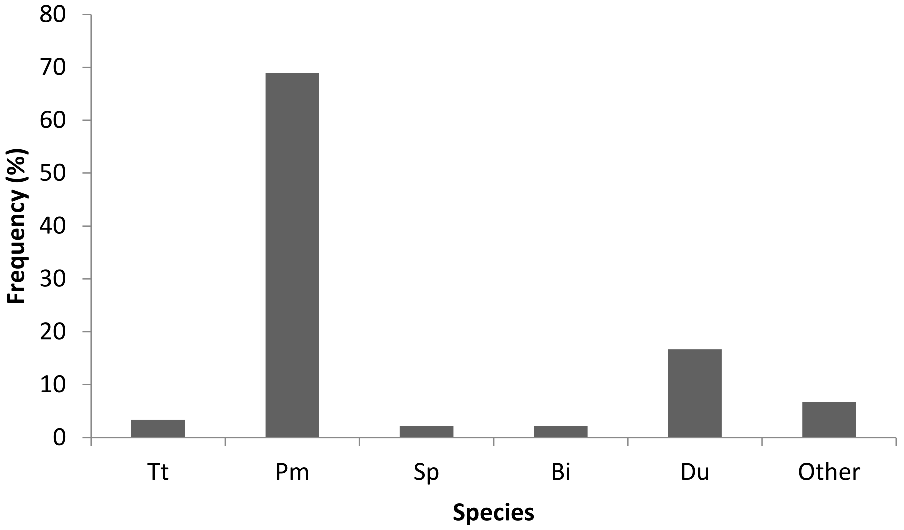

Figure 4.6: the overall grass species composition in the thickets for both treatments (frequency %). Where *Themeda*= *Themeda triandra*, *Panicum*= *Panicum maximum*, *Sp*= *Sporobolus pyramidalis*, *Bi*= *Bothriochloa insculpta*, *Du*= *Dactyloctenium australe*, Other= Bare ground and forbs

Table 4.1 suggests that the fuel load leading up to the trail had no significant effect on whether the fire stopped at the thicket boundary. However, the presence of a trail significantly affected whether the fire burnt into the thicket, but the width of the trail had no significant effect. There was a significant positive relationship between the presence of a trail and whether or not the fire burned into the thickets (Table 4.2). Table 4.2 shows that the thickets were ‘protected’ from the fire by the trails 67% of the time (20/30). However, where no trail was present the thickets were burnt 75% (15/20) of the time, while the thickets escaped burning only 25% (5/20) of the time.

Table 4.1: a GLM for whether the fire was able to burn into the thicket for the treatments, trail present and no trail present

Explanatory variables the fire burning into the thicket or not	**Trail present**	**Width of trail (cm)**	**Fuel load (kg/ha)**
Coefficient estimate	-1.8	-0.004	0.000004
Degrees of freedom	48	47	46
SE	0.7	0.005	0.00003
t	-2.7	-0.9	0.1
p	**0.009**	0.4	0.9

Table 4.2: The number of times the fire did or did not burn into the thickets for the treatments, trail present and no trail present (X^2 = 6.75, df = 1, p<0.001)

	Treatment	
Burnt into thicket	**No trail**	**Trail**
No	5	20
Yes	15	10

Figure 4.7 indicates that the grasslands that lead up to the thicket patches, regardless of whether a trail was present or not were able to carry the fire to the thicket patches. Figure 4.8 indicates that when there was a trail present, the thicket patches generally did not burn. When there was no trail present at least half of the thicket patches burnt.

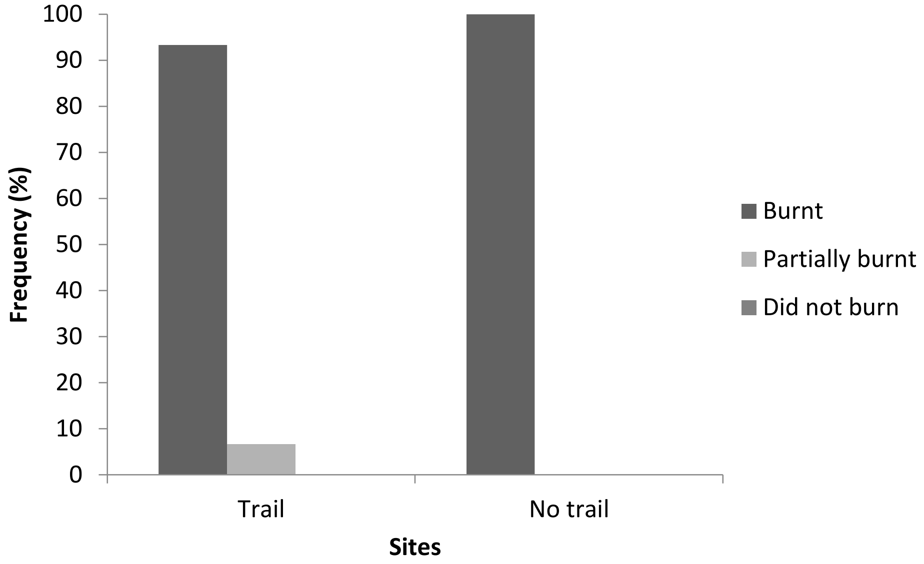

Figure 4.7: the frequency (%) of the grassland leading up to the thicket that did or did not burn for the treatments, trail present or no trail present

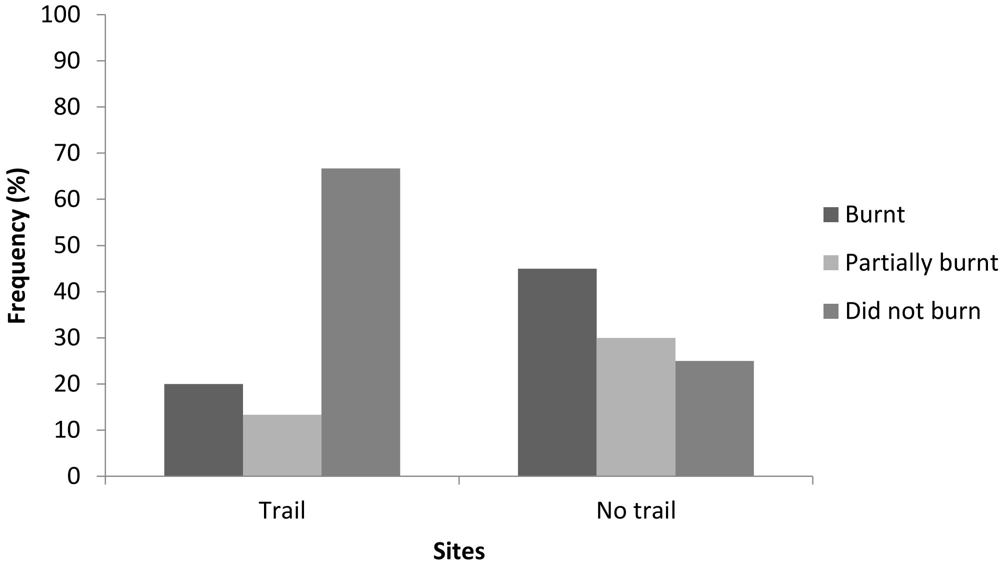

Figure 4.8: the frequency (%) of the thicket that that did or did not burn for the treatments, trail present or no trail present

Discussion

Game trails seemed to have a significant effect on fire behaviour in HiP. The game trails were able to hinder fire spread into thicket patches. Grass fuel loads are important for carrying fires through open savannas into thickets. The grasslands leading up the thickets for both the “trail” and “no trail” treatments had sufficient fuel (around 4000 kg/ha) to carry fire up to the thicket patches (figure 4.4). Although, there was significantly less fuel load present in the thickets, the fires were conducted on a ‘red day’ suggesting that the conditions on the day of the burn could support a fire of sufficient intensity to penetrate into the thickets for both treatments, regardless of the significantly lower fuel loads in the thickets and the dominance of *Panicum maximum* (*Panicum*) in these thickets (figure 4.5and 4.6) (see Chapter 3). This suggests that the significant difference between the sites where trails were present and where trails were not present is primarily due to the existence of these barriers created by animals around these thicket patches.

This conclusion is supported by the GLM analysis, which indicated that the presence of these trails around the thicket edges were a significant factor determining whether fire was able to penetrate into the thicket patches. Surprisingly, the widths of the trails were less important (table 4.1). This may be due to the general size of these barriers; the game trails were mostly larger than one meter in width, which may suggest that they are large enough to act as natural firebreaks.

Table 4.2 implies that there is a significant relationship between the existence of a trail around a thicket edge and whether the fire was able to cross the trail and burn into the thicket area. There was sufficient fuel load for the fire to be carried up to the edge of the thicket patches, regardless of the presence of a trail or not and this is further supported by the fact that all sites were burnt in the grasslands leading up to the thickets (figure 4.7).

Figure 4.7 and table 4.2 suggest that the game trails were able to act as natural fire barriers 67% of the time. In contrast, when there was no trail present, the thickets burned at least on half of the occasions with only about 25% of the samples showing no penetration of the fires into the thickets. This implies that the game trails potentially act as firebreaks and protect the thickets from the fires. The instances where the trails did not protect the thickets or where there was no trail present and the thickets did not burn may be related to biomass or variation in the fire weather at that particular time in the fire.

There may be a "thicket edge" effect reinforcing the "game trail" effect, where there was an increased abundance of *Panicum* (figure 4.5 and see Table 2.1) and a much lower biomass (see Figure 2.3) present in the in the grassland leading up to thicket edges as compared to the typical open savanna *Themeda* dominated grassland, which may reduce the intensity of the fire as it approaches the "thicket edge" (see Chapter 3). Further, the grass species immediately within the edge of the thickets were dominated by *Panicum* (figure 4.6) and had a much lower biomass than the typical *Panicum* dominated grassland (see Figure 2.3) Thus the combination of reduced biomass (fuel load) at the thicket edge and increased abundance of less flammable *Panicum* in the grassland leading up to the thicket edge could hinder the ability of the fire to penetrate the thicket patches.

This suggests a process of assistance where the thicket trees are creating conditions of high shade and increased nutrients in the below-canopy environment (Ludwig *et al*., 2001). This allows for a competitive advantage for woody species and *Panicum* and related species with either PCK C_4 or C_3 photosynthetic pathways which may also have the effect of comparatively reducing the available fuel load (see Chapter 2). The lower flammability of *Panicum* and related species may then reduce the potential for fire to penetrate the thickets. Further, this effect may be mutually reinforced by the presence of game trails that further impede the ability of the fire to penetrate the thickets. These dynamics may be a factor influencing the phenomenon of bush encroachment and raises the question how this may further affect the fire regime in these patchy ecosystems?

Further work would need to be done on the animal effect on thicket margins to elucidate the mechanics of variability in fire behaviour and to further understand the extent that these animal impacts on fire ecology in savanna ecosystems at larger spatial and temporal scales. However, this study indicates that there was an impact of the game trails on fire spread from savanna to thicket. Thus animals appear to be (unknowingly) protecting thicket patches in savanna ecosystems. These short-term site level disturbances may significantly impact the behaviour of the medium term fire disturbance regime on the ecosystem as a whole. These edge effects impacts may be significant contributors to the dynamics of C_3 and C_4 competition and competition within the C4 clade between species with either NADP or PCK photosynthetic pathways. This may affect the species composition, structure and functioning of mesic savanna landscapes.

Chapter 5: Synthesis

Ecosystem properties, whether continuous (such as productivity and other fluxes) or discrete (such as species richness), vary across spatial and temporal scales (Delcourt and Delcourt, 1988; Morgan *et al.*, 1994; Millar and Woolfenden, 1999). Schimper (1903) observed that global vegetation patterns were broadly correlated with climate. This suggested that climatic factors, such as temperature and moisture were the main factors that controlled the distribution of vegetation (Sauer, 1950; Whittaker, 1970; Bond *et al.*, 2003). This assumption has prevailed for at least a century (Beadle, 1966, Specht and Moll, 1983; Bond *et al.*, 2003). Many ecologists observed that grassy ecosystems were not at equilibrium with climate, but rather, they were "deflected from their climate potential" by fire (Bond *et al.,* 2003). However the grassland stage has persisted for hundreds of thousands (millions) of years during which many plant and animal species have evolved to utilise these open fire-maintained habitats (Simon *et al.*, 2009; Maurin *et al.*, 2014). Rather than labelling fire-maintained savannas as 'early successional' to 'climax' forests, they are increasingly described as alternative stable states (Wilson and Agnew, 1992; Bond, 2005; sensu Warman and Moles, 2009; Staver *et al*., 2011; Hirota *et al*., 2011).

The interactions of processes and properties within an ecosystem are extremely diverse and complicated, but may lead to the existence of alternate stable states. Grassy ecosystems, such as savannas, exist under the same climate conditions as forests and thickets and therefore have the potential to exist as alternate stable states (sensu Warman and Moles, 2009; Bond and Parr, 2010). Rapid shifts ('regime shifts') can occur between states (Scheffer and Carpenter, 2003), for example, through extreme events, such as fire. It is postulated that positive feedbacks promote the necessary environmental conditions to maintain a particular ecosystem state and that these conditions are hostile to the alternative ecosystem state. This study begins to delve into these interactions to further the conceptual understanding of how the landscape scale fire regime interacts with site specific game trail disturbances in these grassy savanna ecosystems. As outlined in Chapter one, climate change and elevated atmospheric CO_2 levels may influence the trajectory of grassy ecosystems over a large spatial and temporal scale. This may lead to competition between C_4 and C_3 plants, ultimately, leading to a competitive advantage for C_3 plants. This competitive advantage may be mitigated by landscape scale disturbances, such as fire. However, the trajectory of this mitigation may be influenced by short term and site specific scale disturbances in the landscape.

First and foremost there has been a trend of closed woody vegetation (thicket and forest) invading grassy ecosystems since the 1930s when Henkel mapped the vegetation of Hluhluwe (see Henkel, 1937, figure 2.1). The increase in densely wooded vegetation can be attributed to changes in both local and global drivers (Wigley *et al*. 2010). Among the latter, increasing CO_2 is the most likely candidate since climate change trends in the area have been negligible over the period from the 1930s to early 2000s. The future for African savannas may be strongly influenced by increasing CO_2. Higgins and Scheiter (2012) simulated a major contraction of C_4 grass-dominated vegetation and expansion of trees in the coming century, largely as a result of strong CO_2 effects. Within the grass layer, Collatz *et al*. (1998) predicted a switch from C_4 grass dominance to C_3 grass dominance at atmospheric CO_2 concentrations of ~700 ppm, expected to be reached, perhaps, by the end of the century. If, indeed, elevated CO_2 concentrations influence the comparative relationship between trees and grasses that allow wooded formations to spread, and if C_3 grasses replace C_4 grasses, then there will be massive disruptions to African ecosystems.

Vegetation in Hluhluwe is undergoing two contrasting changes. Over the last century, thicket has increased at the expense of savannas (Wigley *et al.*, 2010). A key question is whether fire can be used effectively to halt further thicket expansion. The other change is the appearance of fire storms, extreme fire events where they are able penetrate deep into closed woody formations from grass-fuelled fires (Browne, 2009). These can be a tool for restoring savannas, or a threat to small patches of forests and thickets. The late dry season 2008 firestorm (Browne, 2009; Browne and Bond, 2011; Wills, 2012) suggests a different future trajectory where extreme weather events trigger catastrophic regime shifts: in this case from forest to grassy ecosystems. Fire storms, followed by a subsequent high frequency fire regime may create the opportunity to reverse the trend of woody plant encroachment. A fire storm can open up the previously stable closed thicket savanna and enable grasses to re-establish dominance in the recovering thicket parts of the landscape. This research tested whether or how a high frequency fire regime can be applied to the recovering thicket area to create a regime shift to an alternate stable savanna state. The study investigated the effect of grass species composition on fire behaviour of the grass sward. *Panicum* and other grasses that dominate in areas that were thicket before the fire storm burn less readily than *Themeda* dominated of the typical open savanna bunch grasslands.

The grass sward in the recovering thicket areas were dominated by less flammable C_4 species, such as *Panicum*. They had a competitive advantage under tree cover over open savanna grass species, including *Themeda*, as there are generally higher soil nutrient and water status conditions in the shade (Kinyamario *et al.,* 1995). Grass species composition strongly influenced the behaviour of fires. With regards to future predictions of woody expansion (Scheiter and Higgins, 2012) and C_3 grasses out competing C_4 grasses at the turn of the century (Collatz *et al.*, 1998), *Panicum* is a sort of proxy for future changes to greener grasses (for e.g. C_3 grasses) in African dry seasons, because *Panicum* allocates a larger proportion of their primary production to above ground live biomass resulting in a higher fuel moisture contents for longer in the dry season. This is an indicator that *Panicum* and related species are less flammable than *Themeda*, which allocates more primary production to below ground biomass during the dry season (Downing and Marshal, 1980).This implies that shifts towards C_3 grasses due to global change drivers, or to less flammable grasses, because of local drivers (*Panicum* recruitment of burnt thicket) will really change fire patterns.

The rates of change of grass species composition needs to be established, since changes in composition seem to affect fire and possibly herbivores. The changes are likely to be quite rapid since *Panicum* occurs in the shade of trees, whereas *Themeda* occurs in the open. So shifts in composition should occur in the lifespan of the trees. A key question is whether an ongoing high frequency fire regime would continue to reduce the canopy cover and give more flammable C_4 species, such as *Themeda*, a competitive advantage. This may induce a species composition to shift towards that of a more typical open savanna.

If the ecological management objective were for C_4 grass species to be allowed to gain a competitive advantage over C_3 woody and grass species, disturbances, such as fire, would need to be employed. Therefore, the fire management protocol would need to achieve burns in the landscape that are complete and intense on a frequent basis. This would deplete the biomass of less desired species through the repeated removal of above ground biomass. For this to be achieved, the differences in the curing rates and biomass between the two grass species would suggest that very late season burns are required in recovering thicket *Panicum* dominated grasslands to ensure complete and intense burns similar to those observed in *Themeda* dominated grasslands. This may be able to restrict the encroachment of woody species typical of the savanna thicket stable state.

This study emphasizes grass species phenology as a key underlying factor influencing the relative flammability of the grassland dominants, other factors may be involved, including the evolutionary history of these grasses, the rate of re-growth after fire (Ripley *et al.*, 2015, in for review). The phylogentic lineage may be more important than the photosynthetic type in determining fire response and fire response may be related to fire frequency of natural habitat (Ripley *et al.*, 2015, in for review). More work is needed in order to confidently predict the consequences of species composition shifts for fire regimes and perhaps savanna landscapes.

In addition to factors affecting the trajectory of change related to the differences in the respective grass species phenology, other site specific scale processes may also be occurring. These may create environmental conditions that impede the ability of fire to direct any shifts between alternate stable states in these savanna ecosystems. The site specific impact of animals in ecosystems may not be as immediately clear and conspicuous as fire. The game trails created by animals and very likely the effects of herbivory (Staver *et al.*, 2009) combined with the mutually reinforcing “edge effect” species composition and biomass (fuel load) dynamics may decrease the effectiveness of fires in achieving shifts from thickets to grassy savanna stable states. Game trail barriers may be acting as natural firebreaks and “protecting” closed thicket patches from fire. This protection effect is mutually reinforced by “edge effect” conditions that enable the potential expansion of the thicket patches through an assistance process. Thicket trees create conditions (shade and nutrients) enabling the establishment of less flammable grasses, including *Panicum* and related species, with typically lower fuel loads, on thicket margins (see Chapter 4). Thus, the ‘edge effect’ adds to the resilience of thicket edges to the impacts of fire by reducing the intensity and completeness of the burn. Over the long-term this would potentially favour the spread of the C_3 woody plants and grasses into the C_4 dominated ecosystems.

The interplay between animals and fire breaks suggests that, as thickets increase, and in the presence of mega-herbivores that are not frightened by thicket patches, it will become more difficult to burn heavily encroached areas. Once again, burning under extreme weather needs to be a part of the fire management tool box for future veld management. The study further supports findings by Govender *et al.*, (2006) that fire intensity and time of the fire in the dry season are important factors governing fire behaviour. Managers of African savannas can manipulate fire intensity by choosing the time in the season to burn, and further by burning in years with higher or lower fuel loads. The precision of the application of these management protocols can be improved through the use of fire behaviour models (Leonard, 2009; Hoffman *et al.*, 2012; Twidwell *et al.*, 2013). Mangers would need to collect the necessary data (weather, biomass and fuel moisture) suitable for the desired fire behaviour predictions.

The dynamics between grass species composition, fire and animals support the alternate stable state theory (sensu Warman and Moles, 2009), where savannas and forests/thickets are in stable states, that are sensitive to changes in prevalent disturbance regimes. A change to a prevalent disturbance regime results in ecological processes and interactions operating at different spatial and temporal scales that drive shifts between alternative states. These dynamics are likely influential in accounting for observed patterns of landscape scale mosaics of savannas, thickets and forests. The results of this study may also support the proposed determinants of the global distribution of savannas and forests as alternative states (Staver et al., 2011). Fire is able to maintain the existing stable states within the context of an underlying long-term trend of increasing CO_2 levels and global climate change, at least for the time being (Staver et al., 2011). However, the outcome of any management interventions aimed at shifting from an ecosystem state favoured under the underlying CO_2 trend to an alternate stable state maintained by a disturbance regime, such as fire, may be variable or uneven and not easily reversible (Staver *et al.*, 2011).This may be due to interactions with other site specific scale disturbances, such as animal impacts, particularly as the underlying CO_2 trend deepens and strengthens.

The effect of animal impacts on the ecosystem and their mutually reinforcing interaction with the observed "edge effect" would need to be further investigated as the frequency of the occurrence of the trails may be influential at larger scales and require additional ecological management interventions to achieve set objectives.

Further research would need to be conducted on the appropriate and safest way to go about conducting high intensity fires in grassy ecosystems. This would include further exploring the flammability of the dominant grassy fuels, so that one may apply the appropriate fire regime to the system. The Working on Fire research team, funded by the South African government’s Department of Environmental Affairs, is currently conducting experiments to develop methods of igniting fires in grassy ecosystems that achieve very high fire intensities safely and effectively. This work is imperative to improve the effectiveness of these protocols, because high intensity fires can spread rapidly and are very dangerous events.

Management recommendations

There is an opportunity here to suggest some basic management guidelines that land managers may use with regards to fire. These recommendations would only seek to improve or clarify management protocols that are already instituted and they would apply according to the management desire of a specific landscape. First and foremost, the management desire would need to be specified. If the management desire were to obtain or maintain a landscape mosaic of open savanna/forest/thicket where the landscape is dominated by open savanna, then the management protocol would be to burn very late in the dry season to obtain high intensity fires and to burn as frequently as possible (every 1 to 2 years). Of course, the opposite should be done if the management protocol is to obtain a wooded landscape or to protect forests. The protocol for that would be to burn very early in the fire season, so that the fuel loads can be kept very low in order to ensure that there is not enough fuel to carry fire into the woody vegetation. However, I would recommend that the frequency of these fires should also be high, so as to control fuel loads. I would recommend using both of the fire models to try to predict what the fire patterns would do in these fires, however, the Trollope & Trollope model does not take into account the slope, so therefore should be avoided when modelling fires on hillsides.

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Appendices

Appendix 1: The dates, times and weather conditions of each of the fire treatments

Fire Treatment	Date	Time	Temperature (°C)	Relative humidity (%)	Wind speed (kph)	Wind direction
Early season	16/07/2013	13:00	29	41	4	South West
Early season	16/07/2013	14:00	24	58	8	South West
Early season	18/07/2014	11:00	26	53	12	South West
Early season	18/07/2014	12:00	26	53	10	South West
Late season	21/08/2013	14:00	32	28	13	South West
Late season	21/08/2013	13:00	32	31	17	South West
Late season	21/08/2013	12:00	31	30	10	South West
Late season	21/08/2013	11:00	31	34	5	South West
Red day	04/08/2014	15:00	31	24	13	North East
Red day	04/08/2014	14:00	32	23	16	North East
Red day	04/08/2014	13:00	32	24	12	North East
Red day	04/08/2014	12:00	32	25	9	North East

Appendix 2: Summary of the average fire behaviour outputs for each species at different times in the fire season

	Themeda triandra			*Panicum maximum*		
Fire type	Fire intensity (kW/m)	Rate of spread (m/s)	Flame heights (m)	Fire intensity (kW/m)	Rate of spread (m/s)	Flame heights (m)
Early season	5078	0.37	3	1173	0.11	1.1
Late season	5465	1	3	2135	0.33	1.6
Red day	4527	0.51	3	2093	0.5	2.4

Appendix 3:BehavePlus5 model parameters used for simulation of fire behaviour (data from van Wilgen and Wills, 1988)

Mon, Oct 22, 2014 at 11:13:49			
Input Worksheet			
Inputs: SURFACE			
Input Variables		Units	Input Value(s)
Fuel/Vegetation, Surface/Understory			
	Fuel Model Type		D (High load, dry climate grass)
	1-h Fuel Load	tonne/ha	Adjusted according to Appendix 4
	10-h Fuel Load	tonne/ha	0.2
	Live Herbaceous Fuel Load	tonne/ha	6.1
	Live Woody Fuel Load	tonne/ha	0.4
	1-h SA/V	m2/m3	6562
	Live Herbaceous SA/V	m2/m3	5906
	Live Woody SA/V	m2/m3	5900
	Fuel Bed Depth	m	0.44
	Dead Fuel Moisture of Extinction	%	20
	Dead Fuel Heat Content	kJ/kg	19500
	Live Fuel Heat Content	kJ/kg	19500
Fuel Moisture			
	Moisture Scenario		d3l1, d3l2, d3l3, d3l4
Weather			
	Midflame Wind Speed (upslope)	km/h	Adjusted for each fire

Appendix 4: The average biomass present in each sub-plot of *Themeda triandra* and *Panicum maximum* at different times in the fire season used in the simulation of fire behaviour in the Trollope and Trollope fire intensity model and the BehavePlus5 model

Fire Treatment	***Panicum maximum* Biomass (kg/ha)**	***Themeda triandra* Biomass (kg/ha)**
Early season	2854	6505
Early season	3491	7242
Early season	4288	7807
Early season	2683	6632
Late season	4689	6441
Late season	3546	7326
Late season	3013	5685
Late season	4639	6377
Red day	3341	5224
Red day	3385	5538
Red day	3153	3984
Red day	2507	3364