

The role of fire in bush encroachment in Ithala Game Reserve

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in the Discipline of Botany

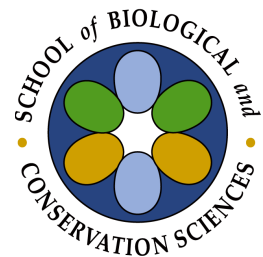
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SUMMARY

The increase of woody vegetation (also known as bush or shrub encroachment) in savannas has become of global concern to conservationists and rangeland managers alike. Bush encroachment has been associated with a decrease in rangeland palatability. In addition, the increase in woody biomass has consequences for climate change, carbon sequestration, rangeland hydrology and nutrient cycling. As a result of these large changes in ecosystem functioning with bush encroachment, biodiversity may be threatened. Fire is considered to be one of the most important management tools used to control woody biomass in savannas. However, despite the use of fire in Ithala Game Reserve, areas have become encroached. This thesis assesses the role of fire in bush encroachment in Ithala Game Reserve.

I start this thesis with a discussion of the bottom-up (water, nutrients, and light) and top-down (fire and herbivory) ecosystem components in the literature review. This sets the foundation for an understanding of the factors that affect savanna tree:grass ratios for the rest of this thesis. In addition the review discusses the potential effects of climate change on savanna tree:grass ratios. Recently, it has been proposed that increasing atmospheric carbon dioxide concentrations result in an increased competitive ability for C₃ woody plants against C₄ grasses. Many models have been produced to explain savanna dynamics. By assessing the role of fire in Ithala Game Reserve, its functioning is assessed in light of the current issues of bush encroachment.

Textural analysis is a remote sensing technique that has been used to detect changes in woody vegetation using aerial photographs. Textural analysis was used to assess changes in woody vegetation cover and density from 1943 (earliest period for which aerial photographs were available for the study area) to 1969, 1990 and 2007 in Ithala Game Reserve (IGR). Field surveys were performed to assess the effects of the fire regime in IGR on woody vegetation structure and composition. Transects were performed in areas with different fire frequencies. The effects of fire frequency were compared between similar vegetation communities.

Textural analysis showed that woody vegetation cover (+32.5%) and density (657.9 indiv. ha⁻¹) increased from 1943 to 2007. Importantly, in some areas of IGR, the suppression of fire led to the rapid invasion of woody plants from 1990 to 2007. Field studies demonstrated the importance of fire in controlling woody vegetation in IGR. The densities of the encroachers, *Dichrostachys cinerea* and *Acacia karroo* were resistant to annual burns. However, the height of these deciduous microphyllous woody encroachers was reduced by more frequent fires. Following the suppression of fire, these trees grew taller and their negative impact on the herbaceous layer increased. Consequently, fuel loads (grassy biomass) declined and prevented the use of frequent and intense fires by management. The reduction in fire frequency allowed the invasion of woody

evergreen macrophyllous species. Continued development of fire-resistant patches of evergreen macrophyllous vegetation will further reduce the effectiveness of fire in controlling bush encroachment.

To control bush encroachment in IGR and the consequential loss of biodiversity, an intermediate fire frequency (one burn every 2 to 4 years) is required. Burns also need to be hot enough to increase the current rate of topkill. Management should act to optimize the accumulation of grassy biomass to fuel fires.

PREFACE

The work described in the thesis was carried out at the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa, from January 2009 to November 2010, under the supervision of Prof. David Ward.

This thesis, submitted for the degree of Master of Science in the Faculty of Science and Agriculture, University of KwaZulu-Natal, Pietermaritzburg, represents original work by the author and has not been submitted in any form to another university. Where use was made of the work of others, it has been duly acknowledged in the text.

Chapter 2 and 3 in this thesis were formatted in the appropriate journal styles that they will be submitted to.



.....
Paul Jan Gordijn
December 2010

I certify that the above statement is correct



.....
Professor David Ward
Supervisor
December 2009

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DECLARATION 1 - PLAGIARISM

I, Paul Jan Gordijn, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
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DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis.

Publication 1 - to be submitted to the International Journal of Remote Sensing

P.J. Gordijn and D. Ward. **Can fire and browsing control bush encroachment?**

Author contributions:

PJG conceived the paper with DW. PJG collected and analysed the data, and wrote the paper. DW contributed valuable comments to the manuscript and facilitated data analysis.

Publication 2 to be submitted to the African Journal of Range and Forage Science

P.J. Gordijn and D. Ward. **Fire suppresses the development of macrophyllous thickets in Ithala Game Reserve**

Author contributions:

PJG conceived the paper with DW. PJG collected and analysed the data, and wrote the paper. DW contributed valuable comments to the manuscript and facilitated data analysis.

Signed:



Paul Jan Gordijn

December 2010

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Chapter 1:

Literature review: An overview of fire and bush encroachment in savannas

Introduction

The ingress of woody plants into grasslands and savannas, commonly known as bush or shrub encroachment, has become an important global concern to rangeland managers and conservationists (Scholes and Archer 1997, Brown and Archer 1999, Britz and Ward 2007a). Rangeland managers and conservationists are concerned about declines in the stocking rates of their land as woody plant densities increase (Hudak 1999, Angassa 2005). For example, in Namibia, bush encroachment has resulted in a loss of 26 million ha of land for raising livestock and may reduce stocking rates by 20 – 30 times in other areas (de Klerk 1999). The ecology of savannas also shifts as the structure and composition of woody plant communities changes, making bush encroachment a significant concern for conservationists (McNaughton and Georgiadis 1986, Dublin 1991, Belsky 1994, Bond and Archibald 2003).

Vegetation structure and composition can however be expected to be dynamic (Eckhardt *et al.* 2000, Meyer *et al.* 2009, Sankaran *et al.* 2008). What concerns conservationists is the large shift in ecosystem service functions and loss of biodiversity, as a result of a reduction in grassy biomass in savannas (Bond and Archibald 2003, van Wilgen *et al.* 2004, Ward 2005). Furthermore, with increasing anthropogenic pressure on rangelands and the rapid rate of land degradation, the fragmentation and reduction of conservancy areas has to be avoided (Pressey *et al.* 2007, Wessels *et al.* 2007). Therefore, conservationists have to thoroughly investigate the factors leading to bush encroachment to prevent the homogenization of savannas (Ward 2005, 2009).

The determinants of woody cover in savannas have been debated in an attempt to understand the dynamics of tree:grass coexistence (Ward 2005, Sankaran *et al.* 2008). Some important generalisations have however been made between arid and mesic savannas (Sankaran *et al.* 2005). Below ~650mm of mean annual rainfall or in arid savannas, tree cover is limited and increases linearly with rainfall (Sankaran *et al.* 2005). However, in mesic savannas that receive >650 mm of mean annual rainfall, woody cover has not reached its maximum potential as dictated by mean annual rainfall. Instead of water being the principal limiting resource, as in arid savannas,

disturbances play critical roles in the control of woody vegetation in mesic savannas (Higgins *et al.* 2000, Bond and Keeley 2005, Sankaran *et al.* 2008).

In particular, fire as a disturbance has been described as a ““global herbivore,”” emphasising its role in regulating the woody component of savannas (Bond and Keeley 2005). The behaviour of fire is spatially and temporally variable and the effects of fire are dependent on environmental conditions at the time of a burn (Bond and van Wilgen 1996). Consequently, the reported effects of fire on woody vegetation have been variable (Higgins *et al.* 2007). Since fire has been considered an important tool in controlling bush encroachment in mesic and humid savannas (Bond and Keeley 2005), an understanding of the response of vegetation to its fire regime is therefore important for effective management.

More recently, scientists have recognised that the competitive dominance of woody plants over the grassy component of savannas may be enhanced by increasing atmospheric CO₂ associated with global warming (Polley *et al.* 1997, Bond and Midgley 2000, Ward 2010), leading to increased concern relating to the ingression of woody plants into grasslands (Polley *et al.* 1997, Bond and Midgley 2000, Ward 2010). With the hypothesized changes in woody and grassy dynamics associated with global warming, it is imperative that a good understanding of the factors increasing bush encroachment is achieved. The understanding of the dynamics of fire and woody vegetation can then be used to help make effective management decisions that incorporate concerns of bush encroachment and increasing CO₂ levels.

Study site

Ithala Game Reserve (IGR) is located in northern KwaZulu-Natal, South Africa (27°30'S, 31°25'E). The reserve covers 29 653 ha, with the Pongolo River forming the northern boundary of the reserve. Prior to proclamation from 1972 to 1982, some of the topographically flatter areas of IGR were used for crop farming since 1884 (Wiseman *et al.* 2004). Indigenous animals were extirpated by the 1950s as a result of rinderpest and hunting (Wiseman *et al.* 2004). From 1973, a number of animals were introduced into IGR including the megaherbivores, black rhinoceros (*Diceros bicornis*), white rhinoceros (*Ceratotherium simum*), giraffes (*Giraffa camelopardis*) and elephants (*Loxodonta africana*).

Altitude ranges from 320 m a.s.l. at the Pongolo River, to 1 446 m a.s.l. on the southern escarpment plateau. This altitudinal gradient leads to high variance in other abiotic and biotic factors. The landscape types over this altitudinal gradient are complex, ranging from plateaux, scarps, cliffs, deeply incised valleys and floodplains along the Pongolo River (van Rooyen and van Rooyen 2008). Approximately 20% of the reserve has slope gradients that exceed 40°, limiting the

distribution of large mammals (le Roux 1985). The geology comprises Archaean granite exposures, sandstones, shales and mudstones of the Karoo system and igneous dolerite dykes and sills (Figure 2). The soils are closely related to the geology, as many are formed *in situ* with the underlying rocks (van Rooyen and van Rooyen 2008). Granites generally form coarse-grained, nutrient-poor soils. However, dolerites and diabases produce fertile soils with poorer percolation compared to that of granite-derived soils (Hillel 1998). The majority of soils are shallow, rocky (lithosols) of the Mispah form. In the extreme eastern section however, the soils are coarse, granite-derived soils (van Rooyen and van Rooyen 2008). IGR is a summer rainfall region with a mean annual rainfall of 781 mm (c.v. = 20.8%). Mean annual temperatures vary from 16.7 – 21.8°C (van Rooyen and van Rooyen 2008).

The vegetation communities of IGR are diverse, ranging from montane grasslands to humid bushveld communities (van Rooyen and van Rooyen 2008). Van Rooyen and van Rooyen (2008) identified 13 plant communities in IGR (Figure 3). In IGR, concern has been raised that a number of woody plants are encroaching (Porter 1983, Kotze 1990, Wiseman *et al.* 2004). The management staff of IGR are concerned that the current fire regime can no longer be used to effectively control woody plant encroachment (Ruinard, pers. comm.). Whatever the factors that have played a part in the role in leading to encroachment, it is imperative that suitable methods are established to slow or stop it, preventing irreversible losses in ecosystem functioning and biodiversity (Bond and Loffell 2001, Bond and Archibald 2003, Bond and Keeley 2005).

The aim of this study is to determine the role of fire in woody vegetation dynamics in IGR. The objectives of this study are to:

- i) assess whether bush density and cover has increased, either before and/or since the proclamation of IGR in 1972,
- ii) to determine the role of the IGR's current fire regime in woody plant encroachment,
- iii) and to assess what the influences of other agents, such as herbivory, may have had on woody vegetation structure and composition.

This study predicts that the density and cover of woody plants has increased from 1943 (when aerial photographs of IGR were first available) until the proclamation of IGR in 1972. Since the proclamation of IGR, this study predicts that the density of woody vegetation has increased in areas where fire frequency has been suppressed. Additionally, fire and other agents such as herbivory have played an interactive role in the changes in woody vegetation structure and composition. Remote sensing data (aerial photographs) were used to assess changes in woody vegetation cover and density using textural analyses (Hudak and Wessman 1998, Hudak and Wessman 2001). Field

surveys were also performed in comparable areas that have experienced different fire frequencies. These field data was used to assess the effects of the IGR fire regime on woody vegetation structure and composition.

This review discusses the development of the models that have been produced to describe woody:grassy savanna dynamics. The bottom-up and top-down factors that affect trees and grass are then discussed so that a better appreciation of fire and its consequences for management can be presented. This literature review provides the relevant information for the results Chapters 2 and 3 presented in this thesis. Chapter 2 is formatted for the **International Journal of Remote Sensing** and Chapter 3 is formatted for **African Journal of Range and Forage Science**. Finally, in Chapter 4 the conclusions are drawn and recommendations for further study are proposed.

Theories of savanna dynamics: Tree: grass coexistence

Savanna ecosystems are comprised of dynamic ratios of trees and grasses. The physiognomy of savannas is diverse, ranging from open grasslands to closed woodlands. Climatically, they are typified by a distinct dry and wet season. Disturbances such as fire have been considered to decrease the height of woody plants (Higgins *et al.* 2000). In mesic savannas, the suppression of fire as a disturbance may shift savannas to a state with increased woody vegetation (Bond and Keeley 2005). As shifts in savanna composition and structure occur, large changes in ecosystem carbon storage and sequestration, rangeland hydrology and nutrient cycling occur (Asner *et al.* 2004, Grace *et al.* 2006, Wigley *et al.* 2010). In addition, conservationists are concerned about the loss of biodiversity as grassland habitat is lost to bush encroachment (Bond and Archibald 2003, Ward 2005).

In an effort to understand and predict changes in the structure and composition of the woody component of savannas, various theories have been developed. As a logical beginning, these theories have attempted to explain the coexistence of trees and grasses in savannas. This question of tree:grass coexistence has become known as the “savanna question” (Higgins *et al.* 2000, Jeltsch *et al.* 2000, Wiegand *et al.* 2006, Bond 2008, Sankaran *et al.* 2008). The theories of tree:grass coexistence in savannas fit into three broad categories based on their assumptions:

i) Equilibrium models hypothesise that tree:grass ratios are stable and disturbances only slightly alter tree:grass ratios temporarily (Walter 1939, Walker and Noy-Meir 1982, Scholes and Archer 1997),

ii) Non-equilibrium models hypothesise that savannas are intrinsically unstable mixtures of trees and grass that persist as a result of disturbances (Higgins *et al.* 2000),

iii) Disequilibrium models hypothesize that there are no stable points that ecosystems tend towards. Savannas governed by disequilibrium dynamics can therefore never reach state of long-term tree:grass coexistence (Jeltsch *et al.* 2000). Typically, disequilibrium models focus on the factors that prevent the transitions from savannas to either grasslands or forests (Jeltsch *et al.* 2000).

Equilibrium models

Classically, it has been assumed that root niche differentiation has enabled stable tree:grass ratios, despite natural variation in rainfall and other disturbances (Walker and Noy-Meir 1982). This differentiation is known as Walter's two-layer model (Walter 1939). According to Walter's (1939) two-layer model, grasses have a competitive advantage over trees as they rapidly absorb moisture in surface soil layers. Trees therefore, as the inferior competitors for water, have to utilize the water inaccessible to the grassy layer in the subsurface soil layers (Walter 1939). The model therefore logically explains why heavy grazing may cause bush encroachment. That is, disturbances such as grazing that reduce grass vigour allow increased water percolation into deeper soil layers, and therefore allow trees to utilize the water in the surface soil layers. This gives woody plants the competitive advantage over grassy components and allows trees to dominate (Walter 1939).

Evidence has been produced that contradicts the parameters of Walter's two-layer model. Some savanna soils are too shallow to allow the required root niche separation for the functioning of the two-layer model (Wiegand *et al.* 2005). The rainfall average and intensity also affects the distribution of water in topsoil and subsoil layers. In periods of above-average rainfall, infiltration to the deeper soil layers increases and may allow some woody plants exclusive access to soil water. However, in periods of average rainfall, infiltration may remain limited by the grassy layer, retarding woody plant growth (Knoop and Walker 1985). In some cases, grasses have been found to have access to subsoil layers, nullifying the root separation of trees and grasses (Knoop and Walker 1985). This model precludes the demography of woody plants, as sapling roots occupy the same soil layer as grass roots (Ward 2005). As a result, Walter's two-layer model has been considered as inadequate and alternative models have been suggested (Ward 2005, Sankaran *et al.* 2008).

An extension of the two-layer model combines the effects of fire, grazing and browsing in the context of tree-grass competition for water (van Langevelde *et al.* 2003). In this model, fire is a disturbance that may alter initial vegetation structure and composition. Increased rainfall results in a higher fuel load for the burning season, that in turn increases the fire intensity (Hudak and

Fairbanks 2004, Bond and Keeley 2005). Both grazing and browsing herbivores are disturbance factors that alter initial vegetation structure and composition (Hawkes and Sullivan 2001, Fritz *et al.* 2002, van Langevelde *et al.* 2003).

Van Langevelde *et al.* (2003) described positive feedback systems with herbivory and fire in savannas. Grazers reduce grassy biomass which consequently reduces the fuel load. The reduced fuel load only allows cooler fires to burn, therefore providing the opportunity for trees to invade. Continued heavy grazing will in time reduce the frequency of fires to the extent that fire may be excluded (van Langevelde *et al.* 2003). Browsing may also influence grass-fire feedbacks. A reduction in browsing intensity results in an increase in woody biomass. Therefore, an increase in the amount of woody plant competition relative to grassy plant competition is expected. The increased competition from woody plants results in a decline in the grassy component. The comparatively unhindered growth of woody biomass is further encouraged by the reduced fuel load and resultant less intense fires (van Langevelde *et al.* 2003).

Whereas Walter's two-layer model (Walter 1939) is based on the premise of niche separation by rooting depth, Scholes and Archer's (1997) model is based on niche separation by phenology (Scholes and Archer 1997). The niche separation by phenology hypothesis emphasises that it is the differential seasonal growth patterns of trees and grasses that allows the persistence of savannas. The typically hot and wet season alternated with dry and warm seasonal shifts of savannas, are concomitant with seasonal changes in vegetation (Note that the assumption of hot and wet summers alternated with dry and warm winters generally applies to the southern hemisphere. In the northern hemisphere where summers are dry and warm, and winters are wet and cold, this model cannot function). Deciduous savanna trees may retain their leaf material for several weeks after grass has senesced. Before the onset of the wet season, deciduous trees may produce new leaf material earlier than grasses (Scholes and Archer 1997). These capabilities of storing and producing photosynthetic materials later and earlier than grasses may provide a mechanism for tree and grass coexistence (Scholes and Archer 1997).

For grasses to persist, they would have to be the superior competitor during periods of simultaneous tree and grass growth (Scholes and Archer 1997). Scholes and Archer (1997) recognized the importance of frequent disturbances that affect competitive advantages between trees and grasses. Disturbances that limit tree establishment such as fire, are therefore hypothesized to provide the mechanism that prevents trees from invading the grassy layer (Scholes and Archer 1997). In this paradigm, with the absence of these disturbances, savannas are expected to be unstable. This means that without disturbances, savannas will generally tend towards a wooded or open grassland scenario, in mesic and arid systems respectively (Scholes and Archer 1997). The

resistance of tree:grass ratio transitions will depend on inherent factors in the environment such as vegetation physiognomy and species composition, rainfall, soil texture and nutrient composition, herbivory and fire regimes (Scholes and Archer 1997). In addition to the intrinsic environmental factors, Scholes and Archer (1997) acknowledged the importance of competition. Notably, there should be stronger intra-life form than inter-life form competition for coexistence of trees and grasses. Inter-tree competitive interactions were important to the functioning of Scholes and Archer's (1997) model. Studies have revealed that strong competitive interactions exist between woody plants in savannas (Smith and Goodmand 1986, Scholes and Archer 1997, Wiegand *et al.* 2006). As woody stands mature and individuals grow, competition for rooting space and resources increases and results in the thinning of tree stands, as weaker individuals are outcompeted (Smith and Goodmand 1986, Scholes and Archer 1997, Wiegand *et al.* 2006). By the natural progression of short dense tree cohorts into less dense, taller tree cohorts, intra-specific competition between trees may facilitate the opening of thickets, and therefore provide opportunities for grasses to invade and coexist with woody plants (Scholes and Archer 1997). The inclusion of multiple environmental variables and life form interactions enabled progression towards complex, but more realistic models (Scholes and Archer 1997).

Non-equilibrium models

Higgins *et al.* (2000) described bottlenecks that limit the recruitment and development of woody plants in savannas. In savannas, the recruitment of woody plants are perceived to be limited by the "bottleneck" of fire or rainfall variability, and disturbance regimes (Higgins *et al.* 2000). The variation in rainfall periods corresponds to variation in tree germination and establishment. Low adult tree mortality (providing trees survive drought periods) allows the persistence of trees in savannas as adults maintain seed banks. This reasoning suggests that mesic savannas are governed by non-equilibrium dynamics (Higgins *et al.* 2000). Higgins *et al.* (2000) based their understanding of savanna dynamics on a model built by Chesson and Warner (1981). For the "storage effect" to work, the longevity of mature woody plants in savannas is important as recruitment is considered limited. The long-lived mature individuals in the population are required to produce seed (Bond and van Wilgen 1996). Seeds then germinate during favourable conditions that may be stochastic, for example due to rainfall frequency (Ward 2005). Once germinated, establishment occurs also under favourable environmental conditions, but disturbance factors generally cause high mortality of establishing woody plants. The "fire trap" describes the disturbance zone < 4 m, within which establishing woody plants are limited by fire-induced topkill (i.e. the death of above-ground biomass) (Trollope and Tainton 1986, Hoffmann and Solbrig 2003). These establishing woody

plants are caught within the “fire trap” so that their recruitment is limited by frequent fires (Bond and van Wilgen 1996, Higgins *et al.* 2000). These woody plants within the “fire trap” have been described as “gullivers,” suppressed by “Lilliputian” grasses that fuel fires (Bond and van Wilgen 1996, Bond and Midgley 2000). In addition, the grasses are direct competitors with woody plants for moisture and nutrients (Knoop and Walker 1985, Riginos 2009, Ward and Esler 2010).

The woody plants that survive living as “gullivers” within the “fire trap” may escape the recruitment bottleneck by growing taller (Bond and van Wilgen 1996, Higgins *et al.* 2000). Once mature, these individuals will then be able to produce seed and contribute to the storage effect by virtue of their longevity (Higgins *et al.* 2000). Although Higgins *et al.* (2000) based their model with fire as the primary disturbance, the similarities of the effects of fire and browsing were also recognised (Prins and van der Jeugd 1993, Higgins *et al.* 2000). Therefore browsing may provide an alternate mechanism for limiting tree establishment and recruitment in savannas (Higgins *et al.* 2000).

Disturbances and episodic recruitment provide the mechanism for tree:grass coexistence and changes in this paradigm. Drought is assumed to limit tree seedlings, while fire and herbivory limit sapling growth. With adequate rainfall for tree establishment in mesic savannas, trees would dominate the landscape, provided that fires were suppressed. In essence, this unstable system may either tend towards open grassland or closed woodland depending on rainfall disturbance regimes (Higgins *et al.* 2000). Therefore, compared to arid savannas, mesic savannas are suggested to be governed by non-equilibrium dynamics that persist as a result of disturbances (Higgins *et al.* 2000).

Disequilibrium models

Jeltsch *et al.* (2000) reviewed articles and books on savanna dynamics and categorised the factors that influence savannas into two groups; i) factors that prevent savanna transition to tropical forest and ii) factors that prevent the transition to an open grassland. This is the basis for their development of the “ecological buffering mechanisms” model (Jeltsch *et al.* 2000).

Fire was found to be an important buffering mechanism that prevents the transition from an open to a more densely wooded or a thicket habitat. The browsing of herbivores was also an important buffering mechanism that may work with fire to prevent the development of forest. Other variables such as grazing were also included, as well as physical factors such as climate and soils. Without these buffering mechanisms, it was noted that savannas with more than 500 mm annual rainfall tended towards a forested biome (Jeltsch *et al.* 2000). The most important factor they considered that prevents the transition of savannas to open grasslands were microsites for tree establishment (Jeltsch *et al.* 2000). Depressions in the soil, termite mounds and seed deposition in

dung are examples of microsites that favour the development of trees, even when frequent fires occur (Owens *et al.* 1995, Barot *et al.* 1999, Jeltsch *et al.* 2000).

By focusing on the buffering mechanisms that prevent transitions to forest and grassland biomes, Jeltsch *et al.* (2000) shifted the focus of the savanna question to the boundaries of its existence. In essence, they argue that savannas exist because there are ecological buffering mechanisms that prevent them from not existing (Jeltsch *et al.* 2000). This shift from an attempt at providing a generalist answer to providing a general framework of analysis is imperative to answering the savanna question. The broadly inclusive term “ecological buffering mechanisms” accounts for the stochastic nature of the environment and spatial and temporal variance between different localities (Jeltsch *et al.* 2000).

Jeltsch’s *et al.* (2000) buffering mechanisms provided a hypothesis that explains the existence of savannas that included their complexity. However, the patch-dynamic model (Wiegand *et al.* 2006) developed more recently, included the necessary theoretical components from other models into a parsimoniously packaged unifying theory (Wiegand *et al.* 2006).

Patch dynamic models

Wiegand *et al.* (2006) developed patch-dynamic models to explain the cyclical progression of an open savanna into a bush-encroached thicket. Patch-dynamics includes both equilibrium and disequilibrium frameworks as it includes concepts from the competition (Smith and Goodman 1986, Scholes and Archer 1997, Wiegand *et al.* 2006) and recruitment-bottleneck (Higgins *et al.* 2000) paradigms. In the patch-dynamics model, the bush encroachment in savannas is considered a natural part of a cycle that returns to an open savanna over time (Wiegand *et al.* 2006). Wiegand *et al.* (2006) acknowledge that the spatio-temporal scale at which field studies are performed will influence the perception of savannas as either stable or unstable (Wiegand *et al.* 2006).

The patch-dynamic model was developed for arid savannas, but also applies to fire-driven savannas (Wiegand *et al.* 2006). In arid savannas, rainfall events are rare and often patchily distributed over time and space (Ward *et al.* 2004). A patch of germinated woody plants therefore occurs in areas with appropriate microsites and importantly, favourable rainfall conditions. Once established, if there is sufficient soil moisture, the woody plants will compete with each other for soil nutrients and moisture. This competition induces self-thinning whereby an encroached patch may revert to an open state over time (Smith and Goodman 1986, Wiegand *et al.* 2006). At their study site in the Pro-Namib, Namibia, Wiegand *et al.* (2005) found that at the landscape level the savanna was in a state of equilibrium, despite the various stages of encroachment at the patch level (Wiegand *et al.* 2005). This emphasises that the scale of an investigation may lead to incorrect

assumptions regarding the stability of a particular savanna. Therefore, patches have to be accounted for in the broad landscape, and different stages of woody plant succession may exist between different patches (Wiegand *et al.* 2006).

In fire-driven savannas, similarly to arid savannas, a recruitment bottleneck exists that prevents the woody plant transition from younger stages to mature size classes (Wiegand *et al.* 2006). Moisture limitations, hot frequent fires, herbivory, and grass competition were considered to limit tree recruitment (Wiegand *et al.* 2004, Wiegand *et al.* 2006). Competition between woody plants is also considered to initiate self-thinning as an encroached stand matures (Smith and Goodman 1986, Wiegand *et al.* 2006, Meyer *et al.* 2008, Wiegand *et al.* 2008). However, fire and herbivory (browsing) may retard the self-thinning process by stunting woody plant growth. Ultimately the cohort of woody plants is expected to return to an open state as it thins through competitive interactions (Wiegand *et al.* 2006, Meyer *et al.* 2008).

In fire-driven savannas the germination to recruitment process occurs in favourable microsites. In addition to the dispersal of seed, edaphic and topographic factors that influence these microsites, fire patchiness is expected to facilitate a patch's recruitment through the creation of open patches (Wiegand *et al.* 2006). Therefore the scale of investigation is also important for fire-driven savannas (Wiegand *et al.* 2006).

Bottom-up Effects

An understanding of the different effects of resources is essential in understanding savanna dynamics (Sankaran *et al.* 2008). The savanna models described above may only be true for a particular set of environment conditions. Therefore, an appreciation of how the availability of resources and their interactions with savanna vegetation is necessary to better understand savanna dynamics (Sankaran *et al.* 2008). The accessibility of nutrients and light that woody and grassy life forms require determine various growth strategies and limitations (Tolsma *et al.* 1987, Belsky 1994, Ludwig *et al.* 2001, Augustine *et al.* 2003, Ludwig *et al.* 2004). Competition for these nutrients results in various tree-grass ratios (Smith and Goodman 1986). It is therefore important to assess bottom-up effects on savanna dynamics, in order to understand the factors that influence initial vegetation structure and composition (Hudak and Fairbanks 2004).

Grasses have dense root networks that allow them to suppress woody plant growth through competition for water and nutrients in the upper soil layers (Bond 2008, Riginos 2009). Generally,

trees frequently have less dense root systems in the top soil but their root systems are more laterally and vertically extensive (Belsky 1994, Scholes and Archer 1997, Meyer *et al.* 2007). Therefore, provided that the soil is deep enough, trees may have exclusive access to water and nutrients (Wiegand *et al.* 2005). Another significant difference between grasses and woody plants is the rate at which they respond to resource increases (Scholes and Archer 1997). Grasses do not have to invest resources in woody stems and can therefore respond more quickly to pulsed resources (Chesson *et al.* 2004). In addition, woody plants have to store sufficient nutrients belowground for resprouting these woody stems (Schutz *et al.* 2009, Wigley *et al.* 2009).

Water

From the early assumptions of Walter's (1939) two-layer hypothesis, water is the resource that allows root niche differentiation and tree:grass coexistence. However, interactions between trees and grass are complex and water may variably affect all demographic stages of trees in savannas (Scholes and Archer 1997, Bond 2008).

Mean annual rainfall has been noted to have an important effect on savanna vegetation. As described above, in areas with >650mm of annual rainfall, disturbances such as fire and herbivory are required to prevent transitions from more open to closed woodlands or evergreen thickets (Sankaran *et al.* 2005). With regard to germination and establishment, frequent, rather than a high average rainfall has been shown to be a critical factor in the germination of *Acacia* seedlings (Garner and Witkowski 1997, Wilson and Witkowski 1998, Witkowski and Garner 2000, Ward 2005, Kraaij and Ward 2006).

The position of the seed, i.e. burial or on the soil surface, has been shown to affect germination by indirectly influencing water potential (Garner and Witkowski 1997, Witkowski and Garner 2000). The stochastic occurrences of favourable rainfall events limits seed germination and establishment, resulting in a demographic bottleneck in arid savannas (Higgins *et al.* 2000, Wiegand *et al.* 2004, Wiegand *et al.* 2006). These favourable rainfall events for woody plant establishment are required in disequilibrium and non-equilibrium models (Jeltsch *et al.* 2000, Wiegand *et al.* 2006). A shortage of water has been recorded to result in the death of seedlings and mature trees (Mueller *et al.* 2005, Bond 2008).

Acacia species have been reported to alter diel soil hydrology by the phenomenon known as hydraulic lift (Ludwig *et al.* 2003). This process mainly occurs at night when plant stomata are closed. A water potential gradient exists from deeper, wetter soils to drier, surface soils. Water then travels along this water potential gradient through the roots of plants and passes into the surrounding soil surface layers by osmosis (Scholz *et al.* 2002, Ludwig *et al.* 2003, Espeleta *et al.*

2004). Ludwig *et al.* (2003) concluded that the hydraulic lift facilitated by *A. tortilis* had limited beneficial effects for grasses. This is because the tree:grass layer absorbs more water from the upper soil layers during the day than is exuded by night. The exact facilitation or competitive relationships with hydraulic lift is likely to be more complex and dependent on the unique morphology and physiology of different tree and grass species (Espeleta *et al.* 2004). Additionally, some *Hyparrhenia* grass species have roots that penetrate 1.5 m deep into soils and therefore could exhibit their own hydraulic lift (Knoop and Walker 1985, Espeleta *et al.* 2004). Perhaps a more important implication of the hydraulic lift phenomenon could be the mineralization effect of water, and consequential availability of nutrients to trees and grasses (Espeleta *et al.* 2004).

Nutrients

Nutrient availability and the various strategies of nutrient acquisition of plants are important determinants of savanna structure and composition (Cramer *et al.* 2010). Nutrient availability in soils is primarily dependent on soil temperature and moisture availability (Jenny 1994). An increase in temperature has a positive effect on the rate of nutrient cycling (Jenny 1994). Moisture availability determines the vegetative growth of plants and consequential carbon inputs into soil, rates of mineralization, leaching of soils, and the availability of nutrients in soils (Cramer *et al.* 2010). Many savanna plants may further modify nutrient availability (Hillel 1998, Cramer *et al.* 2007, Cramer *et al.* 2010).

In mesic savannas, nutrients such as nitrogen (N) and phosphorus (P) have been considered to be the principal limiting resources (Smith and Goodman 1986, Ward 2005, Kraaij and Ward 2006, Britz and Ward 2007b). Legumes (for example some *Acacia spp.* and *Dichrostachys cinerea*) are however able to fix N through nodulation. The importance of N fixation in savannas has been highlighted in a mesic savanna in South Africa. While only 17.5% of the tree species in the mesic Hluhluwe-iMfolozi nature reserve (KwaZulu-Natal, South Africa) were legumes, 77% of the individual trees per hectare were legumes (Cramer *et al.* 2007). Nodulation by legumes does however cost in terms of carbon, and therefore is costly for plants to fix N. Therefore, N fixation by savanna woody plants may only occur when N is limited, either by competition from grasses or in soil nutrients (Cramer *et al.* 2007, Cramer *et al.* 2010).

Light

Sunlight is the principal energy resource for plant life and plants will compete for it as they establish (Smith and Huston 1989, Holmgren *et al.* 1997). Provided there is little or no disturbance, self-thinning will take place as competition for nutrients and light increases (Mohler *et al.* 1978,

Wiegand *et al.* 2006, Wiegand *et al.* 2008). During this process, the different plant species that are adapted to specific microenvironment conditions, will colonise the gaps in the canopy and the various sub-canopies (Scholes and Archer 1997, Reynolds and Ford 2005). As shading becomes more intense, seedling establishment decreases and the vegetation physiognomy will progress towards larger, more widely spaced individuals (Reynolds and Ford 2005, Wiegand *et al.* 2006).

The composition of encroached thickets may change as individuals grow and shading increases (Hoffmann and Franco 2003). Most deciduous microphyllous woody plants are shade intolerant compared to evergreen macrophyllous woody plants (Hoffmann and Franco 2003). Evergreen macrophyllous woody plants also grow taller than deciduous microphyllous woody plants (Hoffman *et al.* 2003). Therefore, evergreen macrophyllous woody plants may invade thickets and shade out deciduous microphyllous woody plants (Hoffmann and Franco 2003, Hoffman *et al.* 2003). This shading out of most deciduous microphyllous woody species shifts the composition of savanna woody communities to evergreen macrophyllous thickets (Hoffmann and Franco 2003, Hoffman *et al.* 2003).

Competition

Competition for different resources between and within grassy and woody plants has been recognised as an important driver of savanna dynamics (Smith and Goodman 1986, Scholes and Archer 1997, Wiegand *et al.* 2005, Meyer *et al.* 2008, Riginos 2009). The relationship between grasses and trees and the nutrients they compete for is complicated (Cramer *et al.* 2010). The limitation of one resource may reduce the efficiency of use of another resource (Raven *et al.* 2004). For example, nitrogen limitation has been shown to reduce the water use efficiency of plants (Raven *et al.* 2004). Other factors such as the seasonal availability of water, herbivory, seasonal shifts in competitive and facilitative interactions (Veblen 2008), and investment strategies of plants have added to the complexity of inter and intra tree:grass interactions (Scholes and Archer 1997, Aerts 1999, Veblen 2008). The suppressive effect of grasses on tree seedlings, saplings and adults through competitive effects for nutrients is apparent in most savannas (Cramer *et al.* 2007, Riginos 2009, Cramer *et al.* 2010, Ward and Esler 2010). Riginos (2009) found that grass competition suppressed all demographic stages of tree growth. When grass was removed, tree growth rates doubled for all tree age classes (Riginos 2009).

For establishing trees, the vigour of the grassy layer is important (Riginos 2009). A healthy grass sward may limit the ability of woody plants to germinate and establish, therefore controlling the density of woody plants (Hagenah *et al.* 2009, Riginos 2009, Cramer *et al.* 2010). As woody plants establish, inter-tree competition has been noted to have an important effect on woody plant

density and structure (Smith and Goodman 1986, Wiegand *et al.* 2006). Wiegand *et al.* (2006) incorporated the effects of inter-tree competition and resultant self-thinning in their patch-dynamic theory. The self-thinning was described as an integral part of savanna dynamics whereby a bush-encroached patch may revert to an open savanna over time (Wiegand *et al.* 2006).

In mesic savannas, disturbances such as fire and herbivory have been described as integral components that prevent the transition from open to closed woodlands (Bond and Keeley 2005, Sankaran *et al.* 2008). The resistance of some thickets and closed woodlands to fire may however extend their longevity (Skowno *et al.* 1999, Hoffmann *et al.* 2003).

Top-down Effects

Grasses not only respond more quickly to pulsed resources than woody plants, they also respond more quickly to fire and herbivory (Bond 2008). Some of the positive feedbacks between fire and herbivory presented by van Langevelde *et al.* (2003) have been described above. These interactions involving woody and grassy vegetation, and fire and herbivory, necessitate an understanding of their dynamics when managing rangelands (Bond and Archibald 2003). It has been proposed that disturbances create an important bottleneck to the establishment of woody plants in savannas (Higgins *et al.* 2000). However, particular suites of disturbances and environmental conditions may shift savannas either to more wooded or open states (Jeltsch *et al.* 2000).

Impacts of Herbivory

African savannas support the most diverse assemblages of browsing herbivores (consume woody biomass), grazing herbivores (consume grassy biomass) and mixed-feeders (consume woody and grassy biomass) in the world (McNaughton and Georgiadis 1986). Herbivores may either directly or indirectly, have a positive or negative impact on woody biomass (Ward 2005, Midgley *et al.* 2010). They may also alter woody species composition through selective feeding (Bond and Loffell 2001, Wiseman *et al.* 2004). The type and stocking density of herbivores influences their impacts on woody vegetation dynamics (McNaughton and Georgiadis 1986, Prins and van der Jeugd 1993, Augustine and McNaughton 1998, Roques *et al.* 2001).

Herbivores select forage on several temporal and spatial scales, depending on the quality and availability of resources (Senft *et al.* 1987). Larger herbivores require more resources than

smaller herbivores because of their greater energy requirements (du Toit and Owen-Smith 1989). Therefore, increasing the density of larger herbivores may have greater impacts on vegetation because of their greater intake requirements (du Toit and Owen-Smith 1989). Furthermore, large herbivores are capable of biting off thicker stems, while small herbivores may only remove leaves. Muzzle or “incisor arcade” size is another related factor that has been linked to the selectivity and impact of herbivores (Gordon and Illius 1988). Herbivores with smaller muzzles are able to select plant parts on a finer scale (Jarman 1974, Gordon and Illius 1988).

Body size or height is also related to the preferential feeding height of browsing herbivores (du Toit and Owen-Smith 1989). Smaller browsers are restricted to feeding at lower levels while larger browsers have access to forage higher in tree canopies. The stocking rates of herbivores across the body size spectrum have important consequences for the structure and composition of woody vegetation (Owen-Smith 1985, Woolnough and du Toit 2001, Danell *et al.* 2006).

Impacts of browsers on woody plants

The broad range of plant responses to herbivory suggest that there is a cost involved for the plants (Strauss *et al.* 2002). However, herbivory may also be beneficial for plants and stimulate plant growth (McNaughton 1983, Paige and Whitham 1987, Hobbs 1996) and provide an agent for seed dispersal (Miller and Coe 1993, Walters *et al.* 2005).

Woody plants have adapted to tolerate herbivory. They have growth characteristics that allow them to compensate for lost tissue (McNaughton 1983), or store nutrients below ground where they are inaccessible to most herbivores (Bond and Midgley 2001). Many savanna species are able to resprout or coppice in response to branch or stem removal, and other physical disturbances of herbivores (Bond and Midgley 2001, Neke *et al.* 2006, Wigley *et al.* 2009). The ability of the browsed plant to survive depends on a number of factors that influence the cost of herbivory. Moderate levels of browsing on shoot tips stimulate rapid recovery of browse-adapted species with adequate nutrients. Repeated frequent browsing may however reduce the vigour of woody plants and without sufficient recovery periods, mortality will occur (McNaughton 1983, Pellew 1983a, Stuart-Hill 1985, du Toit 1990).

Woody plants avoid herbivory by physical and chemical means (Gowda 1997, Rohner and Ward 1997). Physically, plants may grow in locations that herbivores avoid, or decrease their relative preference and/or visibility, i.e. grow in the presence of more preferable species (Hjältén *et al.* 1993). They may also grow taller such that their canopy is inaccessible to browsing herbivores (Allcock and Hik 2004). The development of spines and thorns that deter herbivores is another

physical adaptation prevalent in many African savanna trees such as *Acacia* species (Gowda 1997, Rohner and Ward 1997, Strauss and Agrawal 1999).

Trees and shrubs have also developed chemical defences against herbivory (Gowda, 1997, Rohner and Ward 1997, Ward and Young 2002). As a result, certain plants are avoided by herbivores because of their reduced palatability (Cooper and Owen-Smith 1986). The main compounds that are produced by woody plants to deter herbivores are secondary metabolites. These compounds may function to simply deter herbivores by altering the taste and smell of the plant (Bryant *et al.* 1991, Provenza 1995). Tannin compounds are examples of secondary metabolites that may inhibit protein digestion (Cooper and Owen-Smith 1985, Provenza 1995). In African savannas, an array of herbivores is adapted to forage on woody plants by different methods. These range from the bark-removal habits of porcupines (Yeaton 1988) to the widely documented damage of elephants (Guldmond and van Aarde 2008), from tree felling, root damage and removal, branch damage and removal and bark removal of trees and shrubs (Buss 1961, Danell *et al.* 2006).

The physiognomy of woody vegetation is sensitive to herbivory. Browsing reduces the height and growth rates of plants such that repeated browsing may maintain shrubs and trees at a certain height (Pellew 1983b). To produce seed for sexual reproduction, woody plants have to survive or grow to maturity. For example, selective browsing of *Acacia* species decreases the proportion of a particular species' ability to produce seeds (Goheen *et al.* 2007). The decrease of seed production consequently reduces the proportion of seedlings that may establish themselves (Goheen *et al.* 2007).

Another important factor that is influenced by herbivory is the competitive ability of species with respect to the plant community (Tilman 1988). Herbivory may reduce the ability of plants to compete with neighbouring individuals. This is because the cost of herbivory has to be compensated for. Therefore, a browsed plant loses nutrients, which may reduce its relative competitive ability (Smith and Goodman 1986, Tilman 1988, Gough and Grace 1998, Danell *et al.* 2006).

Impacts of herbivores on grasses

The impacts of herbivores on grasses have cascading consequences for ecosystem processes (Hobbs 1996, Amiri *et al.* 2008). It is therefore important to consider the impacts that herbivores have on grasses and the indirect consequences for woody plants in savannas (van Langevelde *et al.* 2003, Riginos 2009). Frequent defoliation or defoliation without sufficient recovery periods, has been shown to decrease grass vigour (Ferraro and Oesterheld 2002). The decreased grass vigour means

that there is a reduction in the growth rates of roots and lateral tillers (Crider 1955, Mullahey *et al.* 1991). Decreased grass vigour results in an increase in the competitive ability of woody plants relative to grassy plants. Therefore, a decrease in grass vigour has been known to increase the relative growth rates of woody plants (Cramer *et al.* 2007, Riginos 2009). These observations concur with the predictions of Walter's (1939) two-layer model that the grazing actions of herbivores facilitate woody plant establishment.

In general, under moderate grazing pressure with adequate resting periods, the grass sward remains vigorous (Oesterheld and McNaughton 1991). However, under intense utilization, less palatable pioneer grass species dominate and will replace more palatable perennials with less palatable annuals (Westoby *et al.* 1989).

Another impact of herbivores on the grasses and forbs is trampling. Trampling is the term used to describe the mechanical effect of herbivores' hooves on the vegetative and edaphic components of an ecosystem (Danell *et al.* 2006, Savadogo *et al.* 2007). Trampling can destroy the roots or rhizomes of grasses and therefore reduce their vigour and create gaps for woody plant seed germination. Grazing may have analogous effects to the trampling action of herbivores (Danell *et al.* 2006, Savadogo *et al.* 2007). By reducing shading and providing niche gaps for woody plants, both grazing and trampling may have positive effects on woody plant germination. It is therefore generally understood that grazing has a positive relationship with woody plant seedling establishment (Danell *et al.* 2006, Savadogo *et al.* 2007).

Impacts of fire

Fire is a principal tool in managing savannas (Bond and Archibald 2003, Hudak and Fairbanks 2004). The effects of fire are analogous to a generalist herbivore, consuming both grassy and woody biomass (Bond and Keeley 2005). Without fire as a disturbance, open savannas have developed into woodlands and evergreen thickets (also known as gallery forests (Gignoux *et al.* 2009)). In fact, many mesic savannas in Africa are constituted by open savanna – woodland – evergreen thicket mosaics whose boundaries are delimited by fire (Hoffmann *et al.* 2003, Nangendo, 2005, Gignoux *et al.* 2009). Gallery forest trees are more sensitive to fire because of their thinner insulating layer of bark, compared to deciduous microphyllous savanna plants (Hoffmann *et al.* 2003). The gallery forest trees may however be found throughout the open savanna to woodland mosaic, but in low densities (Gignoux *et al.* 2009). Dense thickets and woodlands reduce the fuel (in the form of grassy biomass) available for combustion by shading out

the herbaceous layer (Scholes *et al.* 1996). This suppression of the herbaceous layer may limit the frequency and heat of fires and allow the development of evergreen thickets or gallery forest patches, as observed in southern Africa (Skowno *et al.* 1999).

Fire may also conveniently be used to manipulate local herbivore densities in wildlife systems (Archibald *et al.* 2005). The new green flush of grass growth in burnt areas attracts grazers and focuses the impacts of these herbivores on the burnt area. This provides a direct means to manage vegetation utilization by herbivores on a spatial and temporal scale (Fuhlendorf and Engle 2004, Archibald *et al.* 2005).

Early ideas of fire management were rigid and did not consider the stochastic nature of savannas (Bond and van Wilgen 1996, van Wilgen 2009). Current management philosophy has opted for more variable fire regimes that consider spatially and temporally stochastic processes such as rainfall (Bond and Archibald 2003, van Wilgen 2009). When burning savannas, a number of environmental conditions have to be considered and manipulated to attain the desired fire behaviour (Trollope 1978).

Fire intensity is the energy released when burning and may be practically measured by flame length and rate of spread (Bond and Keeley 2005). The rate of spread is positively related to fire intensity (Byram 1959). Fire severity is another useful measure that describes the ecosystem impact of fires. Tree mortality is commonly used as a measure of fire severity in forested ecosystems (Bond and Keeley 2005). Fire frequency measures the occurrence of fires in an area for a specified duration (Bond and Keeley 2005). A measure related to fire frequency is the fire return interval which describes the time period between fires in a particular area (Bond and Keeley 2005). Fire type is another factor that may be manipulated. Surface fires (the most common type of fires) occur below tall tree canopies, as opposed to crown fires which are carried in the canopies of tall trees (Trollope *et al.* 2002). Two types of surface fires have been used, head burns and back burns. Back burns move towards the general wind direction and head fires move with the wind (Trollope *et al.* 2002).

To manipulate fire intensity, environmental factors such as wind speed, slope, fuel load (grass biomass), type of fire, temperature, humidity and season of burn should be considered (Trollope *et al.* 2002). Wind speed, temperature and fuel load are positively related to fire intensity and humidity has been shown to be negatively related to fire intensity. The intensity of a head burn moving up a slope is positively correlated with slope angle and *visa versa* for back burn (Trollope *et al.* 2002). A head burn moving up slope is able to increase the rate at which fuel preheats directly ahead of itself, increasing the rate and intensity of the burn (Trollope *et al.* 2002). Fires burning down slope decrease the rate of spread and the fire intensity (Trollope *et al.* 2002). Fires later in the

wet season typically have lower dry grass biomass and the relative humidity is greater. Therefore, burns later in the wet season typically have decreased fire intensities. The seasonal timing of the burn may therefore influence fire intensity (Trollope and Tainton 1986).

When managing rangelands it is important to both understand and predict the consequences of decisions. Wildlife managers have a choice of when to burn to select optimal weather conditions, within their desired seasonal limitations. Choices of how often, how much, how intense, when fires are lit, and stocking densities have cascading effects on grass productivity (Scholes and Archer 1997). If grass productivity is too low, insufficient fuel loads will prevent effective burns from controlling bush encroachment (van Langevelde *et al.* 2003). For effective management, the desired outcomes and states of vegetation have to be established (Bond and Archibald 2003). An understanding of woody and grassy plant adaptations and responses to fire and herbivory is therefore mandatory in achieving the desired outcomes (Tainton 1999).

Woody plant responses to fire

Fire is an important factor in regulating savanna woodland dynamics (Bond and Keeley 2005). However, the mortality of savanna trees caused by fire alone is reportedly low (Trollope and Tainton 1986, Midgley *et al.* 2010). It is evident that savanna trees must have adaptations that allow them to survive frequent and intense fires (Balfour and Midgley 2006). Bark thickness has emerged as an important trait of savanna trees for fire protection (Hoffmann *et al.* 2003). Plants with thicker bark are more likely to survive fire (Hoffmann *et al.* 2003). Branch thickness is also an important predictor of topkill (Hoffmann and Solbrig 2003). Branches that are thinner have an increased likelihood of being killed (Hoffmann and Solbrig 2003). Frost is also an important regulator of woody plant dynamics (Sankaran *et al.* 2005, Holdo 2007). The responses of trees to frost damage and fire are similar, suggesting that both agents damage similar plant tissues (Midgley *et al.* 2010).

Coppicing occurs in many savanna species in response to fire and other disturbances such as herbivory (Bond and Midgley 2001). By resprouting, trees are able to produce new shoots and branches so that essential above-ground acquisition of photosynthetic products can continue, promoting survival. To ensure sufficient nutrient reserves for resprouting, many savanna woody plants have below-ground carbon reserves or lignotubers (Bond and Midgley 2001). Resprouting ability is therefore dependent on stored carbohydrate reserves in plant roots, and other undamaged plant parts (Schulz *et al.* 2009). Schutz *et al.* (2009) found that the recovery of root starch concentrations was rapid in *Acacia karroo*. After a fire, burnt *A. karroo* root starch concentrations were half of those of unburnt *A. karroo* plants. The root starch concentrations of the burnt *A.*

karroo individuals recovered within a year. This rapid recovery is imperative for savanna tree species to survive frequent fire disturbances (Schulz *et al.* 2009, Wigley *et al.* 2009, Midgley *et al.* 2010).

Fire typically reduces the height of savanna trees, in addition to causing mortalities (Hoffmann and Solbrig 2003). Woody plants may therefore be stunted in a “gulliver” state (Bond and van Wilgen 1996) until the release of a disturbance enables the escaping of the “fire trap” (Bond and Midgley 2000). As a result of the negative influence of fire on tree height, savanna trees generally mature at a shorter height compared to forest trees (Hoffmann *et al.* 2003). This characteristic allows savanna trees to reach maturity faster and thereby reproduce in the presence of frequent and intense fires (Hoffmann *et al.* 2003). The more branches and stems that are out of the reach of fire, the lower the nutrient reserves needed by plants to invest in resprouting. Stored nutrients can then be invested in maintenance, growth, defence or reproduction (Bond and Midgley 2001, Wigley *et al.* 2009).

Grassy plant responses to fire

Because grasses are effective competitors against trees, the burning regime needs to optimize the negative effects of grasses on woody plants to prevent bush encroachment (Cramer *et al.* 2007). To achieve this, an understanding of the interactions between grasses, fire and herbivory is important (Archibald *et al.* 2005). The effects of fire on vegetation are similar to those of non-selective herbivores (Bond and Keeley 2005). There are however important interactions between grazers and fire that influence grass sward productivity (Archibald *et al.* 2005). The maintenance of a healthy grass sward is important for grass productivity (Trlica and Rittenhouse 1993), soil conservation (Westoby *et al.* 1989, Savadogo *et al.* 2007) and the control of bush encroachment (Riginos 2009). A less vigorous sward recovers more slowly and as a result, insufficient fuel loads accumulate over time. With insufficient fuel loads, fire is ineffective in controlling bush encroachment (van Langevelde *et al.* 2003). The inadequate grass cover of unhealthy swards exposes the soil surface to the mechanical force of rain drops. As a result, soil crusting and runoff increases (Savadogo *et al.* 2007). With increased soil crusting, water infiltration decreases and the consequential increase in runoff results in nutrient losses. Such eroded soils are vulnerable to gully formation and further degradation (Mills and Fey 2003, Savadogo *et al.* 2007). To maintain a vigorous grass sward, fire and grazing events have to be balanced with adequate rest periods (Oesterheld and McNaughton 1991). Importantly, the maintenance of a vigorous grass sward allows sufficient grassy biomass accumulation to fuel frequent and hot fires, for the control of bush encroachment (van Langevelde *et al.* 2003).

Fire behaviour

Fire intensity

Fire intensity, or the energy released by a fire, has been found to have no effect on the grass sward. However, fire intensity influences the effects of fire on woody plants (Trollope and Tainton 1986, Tainton 1999, Walters *et al.* 2004, Govender *et al.* 2006). Fire intensity is positively related to the mortality of woody plants (Trollope and Tainton 1986). However, the mortality of woody plants due to fire alone is reportedly low (Trollope and Tainton 1986, Midgley *et al.* 2010).

Increased fire intensities induce a proportionally greater topkill of woody plants (Trollope and Tainton 1986). Taller plants that have increased stem diameters, compared to shorter plants are however considered to be less vulnerable to stem death (Balfour and Midgley 2006). Relatively small amounts of topkill have been observed in trees ≥ 4 m after intense fires (Trollope and Tainton 1986). At this height, trees are considered to have “escaped” the effects of fire (Trollope and Tainton 1986, Higgins *et al.* 2000).

Season of burn

Season of burn effects both woody and grassy components of savannas (Trollope 1987). To maximise grass yield, burning has typically been done when grasses are dormant. In fire-climax grasslands this has typically been done in late winter to early spring (four weeks before the first rains or two weeks after the first rains) (Everson 1985, Tainton 1999). Burning in spring enables better moisture availability for improved recovery of the grass sward. However, spring burns may expose soil surfaces to the direct negative impact of heavy rains (Everson 1985).

Repeated burning of savannas in early-to-mid winter in wildlife systems is also not conducive to healthy grass swards. Grazing of these areas will be continuous as the nutritious regrowth is attractive to herbivores (Tainton 1999). Such repeated continuous grazing without rest periods will reduce grass vigour and consecutive fuel loads (van Langevelde *et al.* 2003). In fire-climax grasslands, savanna burnt in early-to-mid winter, with a two-year resting interval, has caused a decrease in rangeland palatability (Everson *et al.* 1985). The preferred, palatable grass species are replaced by less palatable grass species under this regime (Everson *et al.* 1985). Despite the negative effects of burning savanna in early-to-mid winter on the grass sward, it is still widely practiced (Everson *et al.* 1985, Tainton 1999).

In the Kruger National Park (South Africa) it has been demonstrated that *Dichrostachys cinerea* is more sensitive to fire damage in the summer (Schutz 2003). This is because the root

carbohydrate reserves of *D. cinerea* are lowest during the summer and post-recovery ability is reduced (Schutz 2003). Other woody species have also been shown to be sensitive to fires in different seasons (Teague and Walker 1988).

Fire type

The type of burn determines the height at which most of the heat of a fire is released (Trollope 1978, Snyman 2002). Back fires burn and release most heat close to the ground, as a result they are the most damaging to the grass sward (Snyman 2002). Head fires conversely have a less negative effect on grass sward recovery and have a higher impact on the topkill of trees. The higher impact of head fires on the tree topkill is explained by the longer flame length, which results in more intense fires. These more intense fires also occur at the height of the above-ground growing points of woody plants, resulting in a higher damage to trees (Trollope 1978, Trollope *et al.* 2002). Crown fires are carried in the canopies of taller trees (Trollope 1978, Snyman 2002).

Fire frequency

The effect of fire frequency is driven by “event-dependent” and “interval-dependent” factors (Bond and van Wilgen 1996). “Event-dependent” effects are driven by factors at the time of the fire such as, fire type, fuel load, and fire intensity. “Interval-dependent” factors are influenced by treatment and growing conditions between consecutive fires. Accordingly, the response of woody vegetation to fire frequency has been difficult to predict and dissimilar trends have been reported (Hoffmann 1999, Higgins *et al.* 2007). There are however some generalizations that have been noted: fire exclusion may allow the development of forest type vegetation with a closed canopy (Bond and Keeley 2005).

The response of tree density to fire frequency is harder to predict. In some areas tree density has decreased, while in others tree density has decreased with increased fire frequency (Higgins *et al.* 2007). Hoffmann (1999) observed that tree density decreased in the Brazilian Cerrado vegetation type with increasing fire frequency. Higgins *et al.* (2007) found that fire frequency had no influence on tree density in semi-arid and mesic savannas. The conflicting trends have been ascribed to differences in the responses to fire of different tree species (Pratt and Knight 1971, Higgins *et al.* 2007, Munkert 2009). In their long-term experiment (40 years), Higgins *et al.* (2007) found that woody plant structure was influenced by fire frequency. The dominance of smaller woody plants (≤ 2 m) was increased in annual and biennial fire treatments. In treatments with triennial burns the dominance of taller trees increased (Higgins *et al.* 2007).

The “event-dependent” and “interval-dependent” effects on fire frequency (Bond and van Wilgen 1996) have produced both increases and decreases in bush densities (Hoffmann 1999, Higgins *et al.* 2007). When using fire to control bush encroachment, it is therefore important to consider the “event-dependent” (e.g. intensity of fire) and “interval-dependent” (e.g. mean return period and grazing regime) factors that may complicate responses of woody plants to fire frequency (Pratt and Knight 1971, Higgins *et al.* 2007, Munkert 2009).

Carbon dioxide

Carbon dioxide levels have increased from 270 ppm during pre-industrial times to current 360 ppm levels (Bond *et al.* 2003). This increase in atmospheric CO₂ has been proposed to increase the competitive advantage of C₃ woody plants over C₄ grassy plants. This has been used to explain the global phenomenon of bush encroachment (Bond and Midgley 2000, Bond *et al.* 2003, Ainsworth and Long 2005, Sankaran *et al.* 2008, Ward 2010, Wigley *et al.* 2010).

Three mechanisms by which trees have an increased competitive advantage over grasses, as a result of increased CO₂ levels are discussed below (Polley *et al.* 1997, Bond and Midgley 2000, Ward 2010). Polley *et al.* (1997) described the effects of the soil water availability shifts on trees and grasses associated with increased CO₂. Bond and Midgley (2000) produced the fire-carbon model, and Ward (2010) used a resource-ratio model to explain why trees have an increased competitive advantage over grasses with increased CO₂. Although these models are not necessarily mutually exclusive, some may hold better in particular environments (Ward 2010). The three main models are described below:

Soil-water availability

The availability of soil water is an important determinant of tree:grass ratios in arid and semi-arid savannas (Sankaran *et al.* 2005). It has been shown for many C₃ and C₄ plants that stomatal conductance decreases with increasing CO₂ concentration (Field *et al.* 1995, Polley *et al.* 1997). The decrease in stomatal conductance corresponds to a decrease in transpiration, provided this is not offset by an increase in leaf temperature and leaf area. The decrease in transpiration facilitates improved water percolation into deeper soil layers. Therefore, trees that have access to deeper soil layers will have increased water availability with the higher CO₂ levels predicted by global climate change (Polley *et al.* 1997).

This prediction of increased water availability to trees assumes that trees have access to deeper soil layers. This is not the case with saplings, as they share rooting space with grasses (Ward 2005). The prediction would therefore only apply to trees of a particular size in an environment that allows root niche differentiation.

Disturbance-carbon model

Bond and Midgley (2000) emphasize the importance of the resprouting niche in environments with frequent disturbances. Herbivory and fire are disturbances that woody plants have to overcome to survive. These disturbances prevent the growth of woody plants to a size that minimizes the negative effects of these disturbances (Bond and van Wilgen 1996). Therefore, woody plants may exist in a smaller size class, or as “gullivers,” for long periods (Bond and van Wilgen 1996).

To survive these disturbances as “gullivers,” woody plants have to be able to resprout. With increased atmospheric CO₂, woody plants can increase the amount of carbohydrate reserves in tubers below ground. The increase in carbohydrate reserves allows better recovery or resprouting ability of woody plants after disturbances. The resprouting ability of woody plants is a critical stage of their demography in savannas (Bond and Midgley 2000, Bond *et al.* 2003). Therefore, the ability of “gullivers” to escape the “lilliputian” suppressive effects of grasses should increase. This helps explain the globally observed phenomenon of increasing woody vegetation in fire-prone environments (Bond and Midgley 2000).

Resource-ratio model

Ward (2010) asserts that C₃ trees will be able to invest more in plant defences and grow faster relative to C₄ plants, and therefore increase their relative chances of survival (Ward 2010). The increase in CO₂ will more positively affect the net photosynthetic rate of C₃ plants than the relative photosynthetic rate of C₄ plants (mostly grasses) (Wolfe and Erickson 1993). Therefore, C₃ plants will be able to grow faster relative to C₄ grasses (Ward 2010).

In addition to the increased growth rate of trees compared to grasses, Ward (2010) predicts that the higher CO₂ levels will allow woody plants to increase their carbon-based defences. Tree species such as acacias may therefore increase both their physical (e.g. spines) and chemical (e.g. condensed tannins and other polyphenols) defences and reduce their loss rates to herbivory (Ward 2010). These extra defences will improve the loss rates of acacias to herbivory and therefore improve their relative competitive ability against grasses.

Using Tilman’s (1982, 1988) resource-ratio or R* model, Ward (2010) explained how trees may outcompete grasses under the increased CO₂ levels predicted by global warming. The

resource-ratio model denotes that R^* is the resource level that denotes a zero net rate of population change for a species (Tilman 1982, 1988). Ward (2010) demonstrated that with increased net photosynthetic rates, C_3 plants will have reduced R^* because of increased growth rates and decreased losses to herbivory. These lower R^* values of C_3 give them a competitive advantage over C_4 plants, allowing C_3 plants to grow faster (Ward 2010). Therefore, with increased CO_2 , Ward (2010) predicts that trees will outcompete grassy plants. Therefore, with increased growth rates and increased defences, Ward (2010) predicts that woody plants will encroach as CO_2 increases regardless of whether environments are fire-prone or not.

Although these three models are based on different premises, they are not necessarily mutually exclusive (Ward 2010). Polley *et al.*'s (1997) application of the soil-water availability hypothesis (Walter 1939) to increasing CO_2 levels applies to savannas where tree:grass root niche differentiation is evident. The assumption that decreased transpiration rates of grasses and resultant deeper percolation of water implies that the tree:grass root niche differentiation hypothesis of Walter (1939) is operative (Polley *et al.* 1997). In some savanna areas it has been shown that the soil layer is too shallow for root niche differentiation of trees and grasses (Wiegand *et al.* 2005) and therefore violates the assumption necessary for Polley *et al.*'s (1997) prediction.

Bond and Midgley's (2000) disturbance-carbon model assumes that savanna plants, in particular "gullivers," are prevented from escaping the "topkill" zone by disturbances such as herbivory and fire (Bond and Midgley 2000). Many woody species exhibit resprouting behaviour in response to disturbances (Bond and Midgley 2001). Thus, resprouting behaviour and disturbances are necessary assumptions of Bond and Midgley's (2000) disturbance-carbon model. Ward's (2010) model is more general in application. An assumption of Ward's (2010) resource-ratio model that differs from the disturbance-carbon model (Bond and Midgley 2000) concerns the concentration of CO_2 . The disturbance-carbon model is effective in the CO_2 concentration range where Rubisco-based photosynthesis is strongly limited (~100 to ~450 ppm) (Bond and Midgley 2000). The resource-ratio model is likely to function at CO_2 concentrations (≥ 450 ppm) where C_3 plants have higher net photosynthetic rates than C_4 plants (Ward 2010). Both the Bond and Midgley (2000) and the Ward (2010) models described above may be operative, provided the environmental conditions are satisfied (Ward 2010).

The separate and collective applications of these models assert that C_3 woody plants have an advantage over C_4 grassy plants with increasing CO_2 levels (Polley *et al.* 1997, Bond and Midgley 2000, Ward 2010). Therefore, they may explain one of the many factors that have led to the globally observed phenomenon of bush or shrub encroachment (Ward 2010).

To verify the some of the hypotheses regarding the effects of increasing CO₂ levels on woody vegetation, controlled glasshouse experiments and field studies have been performed (Körner and Miglietta 1994, Körner *et al.* 2005, Stock *et al.* 2005, Kgope *et al.* 2010). In a glasshouse experiment, Kgope *et al.* (2010) have demonstrated the effects of increased CO₂ levels on the C₃ trees *A. karroo* and *A. nilotica* and the C₄ grass *Themeda triandra*. Along an increasing CO₂ concentration gradient, the photosynthesis, total stem length, total stem diameter, shoot dry weight and root dry weight of the acacias increased significantly. For *T. triandra* however, there was no significant response to increased CO₂ levels (Kgope *et al.* 2010). Clipping of the trees at higher CO₂ concentrations, to simulate fire under increased CO₂ levels, prompted more rapid recovery than at lower CO₂ levels (Kgope *et al.* 2010). This suggests that trees may be able to grow and escape the effects of the “fire trap” faster at higher CO₂ levels. Increased CO₂ levels may therefore reduce the effectiveness of fire in controlling bush encroachment in savannas (Kgope *et al.* 2010).

The experiments by Kgope *et al.* (2010) illustrate the increased competitive advantages of C₃ trees with increasing CO₂ levels, compared to C₄ grasses. This competitive advantage for woody plants, with the positive shift in CO₂ levels, has been used to explain the global increase of woody biomass, at the expense of grassy biomass (Polley *et al.* 1997, Bond *et al.* 2003, Kgope *et al.* 2010, Ward 2010, Wigley *et al.* 2010).

In the field however, the effects of CO₂ enrichment on C₃ trees and C₄ grasses have not been as clear as Kgope *et al.* (2010) found in their glasshouse experiments (Körner *et al.* 2005, Stock *et al.* 2005). For example, Stock *et al.* (2005) found no differences in C₃:C₄ plant abundance ratios that were attributable to long term CO₂ exhalation from a natural spring, in South Africa (Stock *et al.* 2005). Furthermore, increased CO₂ levels had no effect on ecosystem properties such as soil nutrients (Stock *et al.* 2005). The differences between field and glasshouse experiments may be due to confounding factors in natural systems that are absent in closed glasshouse experiments (Körner *et al.* 2005, Stock *et al.* 2005). The reaction of trees to increased CO₂ levels has also been found to vary among species (Körner *et al.* 2005).

Although controlled or glasshouse experiments have demonstrated that the growth rate of some savanna trees may relate positively to CO₂ concentration (Kgope *et al.* 2010), experiments in natural systems imply have not verified these findings (Körner *et al.* 2005, Stock *et al.* 2005). Therefore, the effects of the increased CO₂ levels on savanna woody:grassy plant biomass in natural systems remains uncertain (Körner *et al.* 2005). The application of the described soil-water availability (Polley *et al.* 1997), disturbance-carbon (Bond and Midgley 2000) and the resource-

ratio (Ward 2010) models should therefore be made with caution as they require validation in natural systems (Körner *et al.* 2005, Stock *et al.* 2005, Kgope *et al.* 2010, Ward 2010).

Synthesis

The review of the bottom-up and top-down factors that influence tree:grass ratios in savannas highlights the fact that simple models are inadequate (Ward 2005). In reality, many factors have to be considered when describing dynamic tree:grass ratios in savannas (Scholes and Archer 1997). Each demographic stage of different woody species has to be examined with regards to a particular environment's resources and disturbance regime (Riginos 2009, Midgley *et al.* 2010).

For germination to occur, frequent rather than high rainfall is necessary (Kraaij and Ward 2006). The intrinsic preferred environmental conditions for each species, e.g. rainfall frequency and amount, will dictate the success of germination in different micro- and macro-habitats (Skowno *et al.* 1999). Therefore, the correct germination niche for particular species has to be provided. Similarly, to survive and establish as a sapling, the particular niche for a species has to be available. The intrinsic strategies and capabilities of woody plants at each demographic stage combined with;

- i) resource conditions,
- ii) the vigour and competitive/ facilitative abilities of neighbouring trees and grasses,
- iii) appropriate disturbance regimes,

will determine the survival of saplings and larger trees in a particular plant community (Kraaij and Ward 2006, Bond 2008, Sankaran *et al.* 2008, Riginos 2009, Cramer *et al.* 2010, Midgley *et al.* 2010).

It is important to realise that resource conditions, combined with the competitive and/ or facilitative relationships between and within different tree and grass species will influence vegetation structure and composition (Smith and Goodman 1986). Disturbance regimes also play an important role in the shifts in woody plant community composition and structure. Without disturbances such as fire, mesic savannas have been known to develop into evergreen macrophyllous thickets within a decade (Skowno *et al.* 1999, Bond and Archibald 2003). In addition, thickets and closed woodlands may revert to open woodlands through the action of fire and elephants as disturbance agents (Dublin 1991). The selective damaging behaviour of herbivores may alter the relative competitive ability of woody species. Above certain levels of herbivory, plants are unable to compensate (McNaughton 1983, du Toit *et al.* 1990). At these

levels of herbivory, the less preferred species have a competitive advantage. In this way, woody plant community composition may be altered (Danell *et al.* 2006).

Fire has been considered a generalist herbivore (Bond and Keeley 2005). However, in areas where fire occurs, species that are not adapted to a particular fire regime are excluded. Therefore, the behaviour of fire may be considered to influence community composition through indirect selection (Bond and Keeley 2005). The combination of disturbances and their interactive effects on species is a more powerful determinant of vegetation structure and composition. Together, various disturbances, such as fire and elephant damage (Dublin 1991, Holdo 2007), may drastically alter species' competitive abilities and mortality rates of plant (Holdo 2007, Holdo *et al.* 2009, Midgley *et al.* 2010).

Throughout the literature, the role of fire in woody vegetation has been considered important (Skarpe 1992, Scholes and Archer 1997, Skowno *et al.* 1999, Bond and Archibald 2003, van Langevelde *et al.* 2003, Hudak and Fairbanks 2004, Walters *et al.* 2004, Bond and Keeley 2005, Sankaran *et al.* 2008, Schutz *et al.* 2009, Wigley *et al.* 2009). The behaviour of fire may be manipulated to achieve the desired outcomes. Notably, fire has been used to control the density and structure of savanna woody vegetation (Trollope 1987, Bond and Keeley 2005, Higgins *et al.* 2007). In addition, fire has played an important role in the prevention of the formation of closed woodlands and thickets (Skowno *et al.* 1999, Bond and Archibald 2003, Bond and Keeley 2005).

In Ithala Game Reserve, this study predicts that where fire frequency has been suppressed, there will be an increase in woody vegetation cover and density. The density and height of woody vegetation is also expected to be reduced in areas with more frequent fires. The composition of woody vegetation is also predicted to have been affected by fire. In areas with more frequent fires, the abundance of forest or evergreen macrophyllous trees is predicted to be lower than in areas with lower fire frequencies. Since the proclamation of IGR, the wild browsers introduced into IGR are also predicted to have facilitated a decrease in the density and cover of woody vegetation.

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Appendix 1:

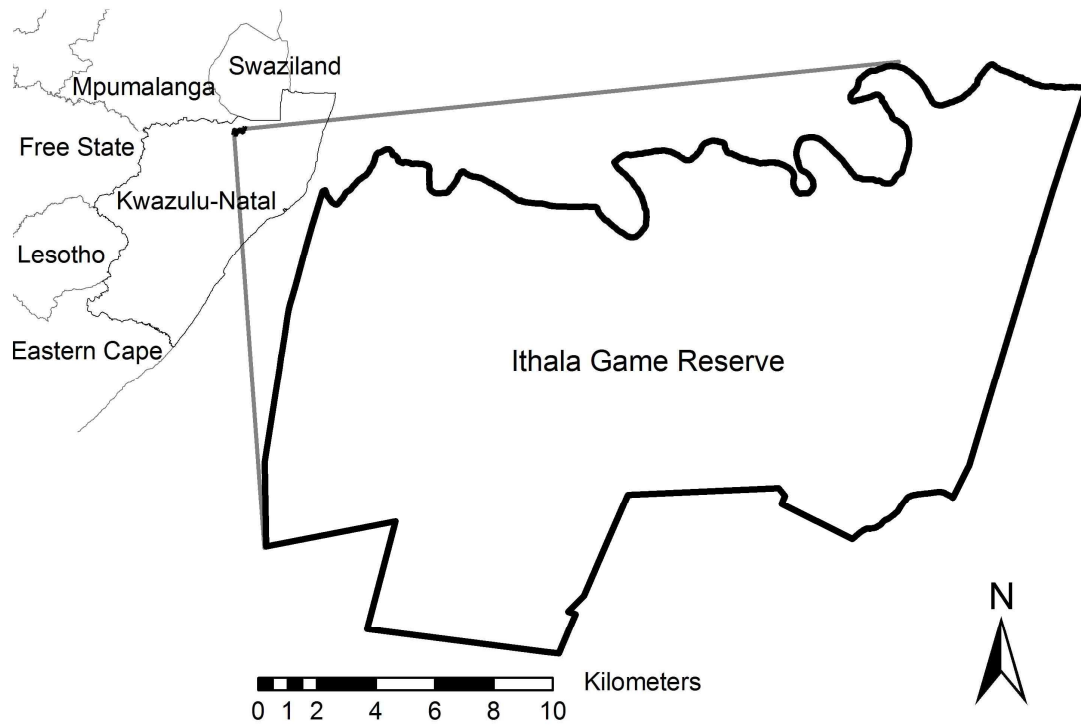


Figure 1: Situation map of Ithala Game Reserve with respect to KwaZulu-Natal in South Africa.

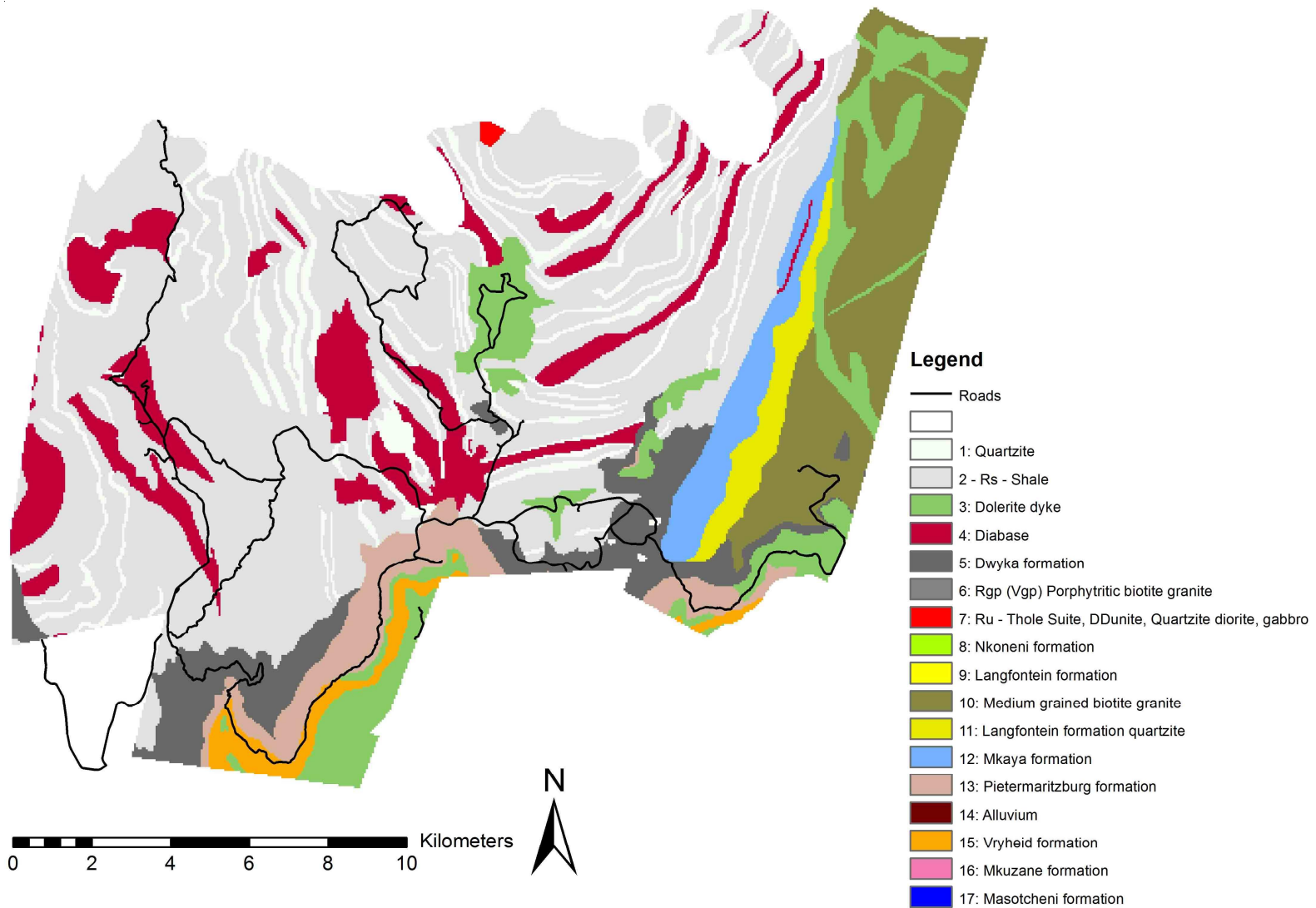


Figure 2: Geology of Ithala Game Reserve (produced from CAD file provided by Ezemvelo KZN Wildlife in Arc Map version 9.2).

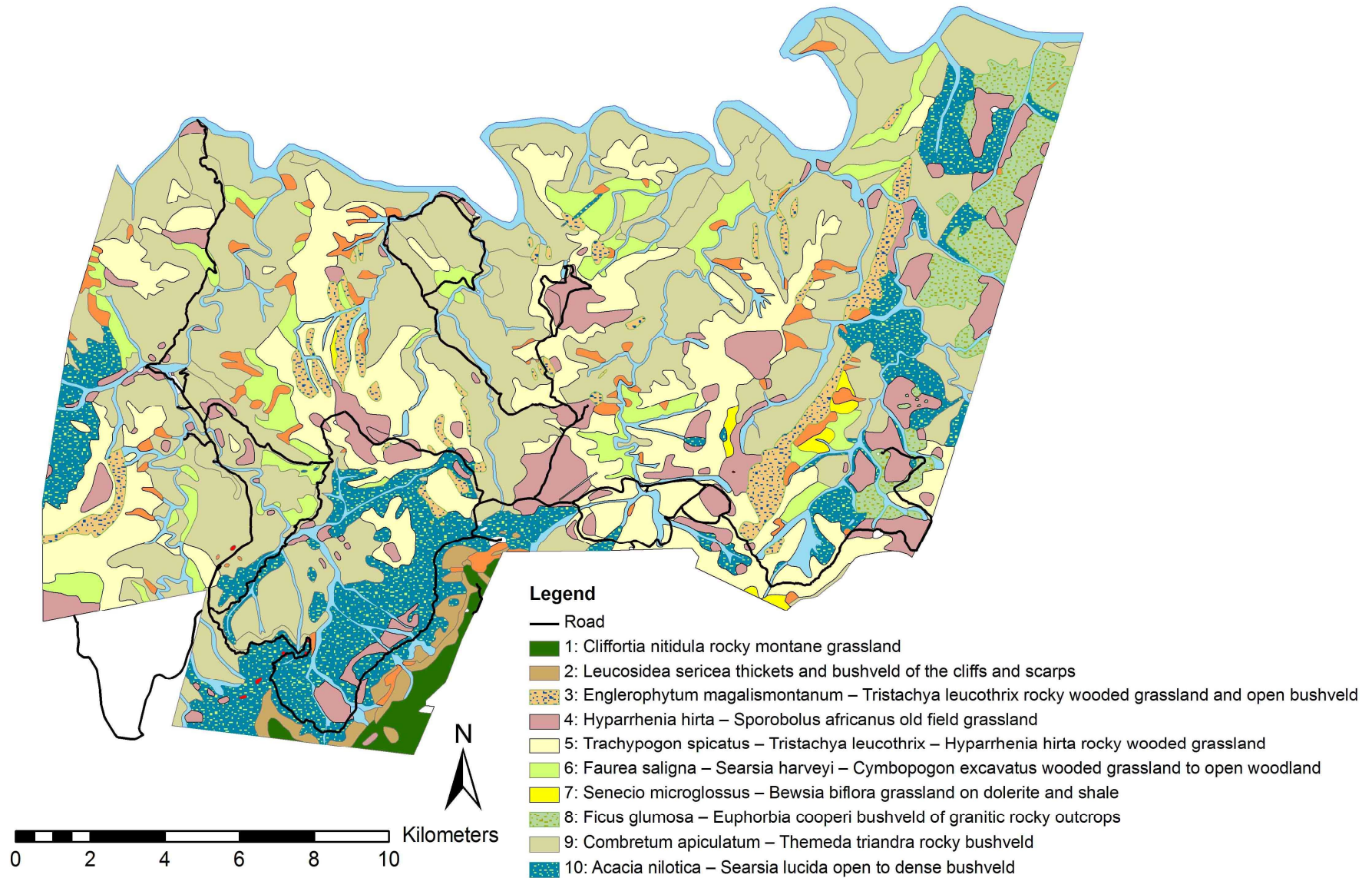


Figure 3: Vegetation communities of Ithala Game Reserve, according to van Rooyen and van Rooyen (2008).

Chapter 2

Can fire and browsing control bush encroachment?

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Abstract

The ingression of woody plants into the grassy layer, known as bush or shrub encroachment, has become a global concern. Fire has been successful in controlling the expansion of evergreen macrophyllous thickets in savanna areas. However, the effects of fire on deciduous microphyllous woody vegetation have been less predictable. Fire may change savanna structure by reducing the height of woody plants. However, the effect of fire on the density of deciduous microphyllous woody plants has been variable. In some savannas, increased fire frequencies have reduced the density of deciduous microphyllous woody plants, while in others no significant effect has been observed. Further complications regarding woody plant encroachment associated with climate change have recently emerged. Textural analysis of aerial photographs was used to detect changes in woody vegetation, from 1943 to 2007 in Ithala Game Reserve (IGR), South Africa. Woody vegetation cover and density increased significantly by 32.5% and 657.9 ind. ha⁻¹, respectively, over the 64 year period. Before the proclamation of IGR in 1972, increases in woody vegetation from 1943 were non-significant. This increase was non-significant as the factors that were positively influencing bush encroachment (increase in grazing by livestock since 1884 and changes in rainfall patterns), were balanced by the factors that control woody vegetation. Prior to the proclamation of IGR, an (i) extended dry period, (ii) anthropogenic tree harvesting, (iii) browsing by goats and (iv) frequent fires controlled bush encroachment. After the proclamation of IGR, herbivore population numbers and spatial distribution influenced the accumulation of grassy biomass required to fuel fires. In areas with reduced fuel loads, the consequential suppression of fire accelerated the rate of woody plant invasion into savannas. The increase in woody vegetation occurred despite the very large increases in wild herbivore populations in IGR since the proclamation of the reserve in 1972.

Keywords: bush encroachment, fire suppression, herbivory, remote sensing, textural analysis

1.1. Introduction

The ingression of woody plants into savannas, known as shrub or bush encroachment, has become a global concern (Scholes and Archer 1997, Brown and Archer 1999, Britz and Ward 2007). The problem of bush encroachment has raised concern for conservationists and commercial rangeland owners. Bush encroachment has been associated with a decrease in palatable grasses and herbs, resulting in a decrease in rangeland palatability (Ward 2005). The conversion of savannas to closed forests also has consequences for the climate, carbon storage and sequestration, rangeland hydrology and nutrient cycling (Asner *et al.* 2004, Grace *et al.* 2006, Wigley *et al.* 2010). In addition, conservationists are concerned about the loss of biodiversity as grassland habitat is lost to bush encroachment (Bond and Archibald 2003, Ward 2005). A number of factors are involved in controlling and facilitating bush encroachment. Water availability or rainfall patterns (Walter 1939, Knoop and Walker, 1985), and disturbances such as fire, grazing and browsing impacts (van Langevelde *et al.* 2003, Wiseman *et al.* 2004) have been shown to influence tree:grass ratios in savannas (Sankaran *et al.* 2005).

Fire has generally been assumed to be a principal limiting agent of woody plant growth (Bond and Keeley 2005). Fire has had a noted effect in controlling the expansion and formation of evergreen macrophyllous thickets (also known as gallery forests (Gignoux *et al.* 2009)) into savannas (Skowno *et al.* 1999, Hoffmann *et al.* 2003, Gignoux *et al.* 2009, Nandengo *et al.* 2006). It has been estimated that the current extent of forests, which is ~25% of the global land surface area (excluding Antarctica), would more than double following the suppression of fire (Bond and Keeley 2005). More recently however, the effectiveness of fire in controlling woody vegetation has been questioned (Higgins *et al.* 2007).

Higgins *et al.* (2000) demonstrated that savanna woody plants are limited by demographic bottlenecks (Higgins *et al.* 2000). Episodic rainfall events are considered to limit the germination and recruitment of seedlings (Higgins *et al.* 2000, Wiegand *et al.* 2006). Fire is the important disturbance that has been described to limit the recruitment of seedlings into taller, mature trees (Higgins *et al.* 2000). By inducing topkill (i.e. the death of above-ground woody plant biomass), fire prevents the growth of woody plants. Higgins *et al.* (2000) showed that savanna trees may escape the effects of fire by growing taller in periods that are favourable for growth (i.e. fire suppression) (Higgins *et al.* 2000).

Fires may prevent the development of closed woodlands (Trollope and Tainton 1986, Higgins *et al.* 2000, Balfour and Midgley 2006).

Higgins *et al.* (2007) used data from a four decade-long fire experiment to assess the effects of fire on woody vegetation in Kruger National Park, South Africa (Higgins *et al.* 2007). They found that more frequent fires alter savanna structure by reducing the height of individuals (Higgins *et al.* 2007). Although savanna structure was affected by fire frequency, the density of woody plants was unaffected (Higgins *et al.* 2007). These results concur with Higgins *et al.*'s (2000) demographic bottleneck model (Higgins *et al.* 2007), which states that savanna trees are resilient resprouters and may exist as short individuals for long periods, despite frequent fires. Therefore, fire may have limited effects on savanna tree density, but rather alter savanna structure (Higgins *et al.* 2007). In contrast, some studies have shown that more frequent fires reduce tree density in savannas (Boulton 1981, Sweet 1982, Hoffmann 1999). The different trends regarding the effects of fire frequency on woody plant density, have called into question the effectiveness of fire in controlling bush encroachment (Higgins *et al.* 2007). Furthermore, factors such as increasing CO₂ levels (associated with global warming), have wrought further doubt regarding the effectiveness of fire in controlling bush encroachment (Higgins *et al.* 2007, Kgope *et al.* 2010).

Herbivores may have significant effects on the encroachment by woody plants. Grazing herbivores (that eat grass only) may remove grass and thus increase the space available for trees to germinate *en masse* (Walter 1939, Savadogo *et al.* 2007). Browsers (that primarily eat trees) may reduce the density of trees, particularly affecting the density of palatable trees (Wiseman *et al.* 2004, Goheen *et al.* 2007, Holdo 2007). Consequently, unpalatable trees may replace palatable trees (Wiseman *et al.* 2004, Holdo 2007). Should all trees be relatively palatable, or there is a suite of browsing herbivores exhibiting differences in their preferences, severe declines in woody plant densities may occur (Wiseman *et al.* 2004, Holdo 2007). Many encroaching species in South African savannas are unpalatable. Of these encroaching species, macrophyllous species such as *Euclea* and *Searsia* (formerly *Rhus*) are more unpalatable than microphyllous species, such as *Acacia nilotica* and *A. gerrardii* (Smith and Goodman 1987, Skowno *et al.* 1999). *Euclea* spp. contain toxic chemicals such as naphthoquinones and triterpenoids, and *Searsia* spp. contain inositol, and malic and nonanoic acids (Hutchings *et al.* 1996).

Apart from fire and herbivory, changes in climate patterns have been predicted to alter tree:grass ratios in savannas (Knoop and Walker 1985, Ward 2010). Water is a principal limiting factor

in savannas and plays a fundamental role in determining the ratio of trees and grasses in savannas (Sankaran *et al.* 2005). Grasses have however been shown to be competitors that are able to suppress the growth of trees in all demographic stages (Knoop and Walker 1985, Riginos 2009, Cramer *et al.* 2010). Grasses limit both nutrient and water uptake by woody plants within similar and different soil layers (Knoop and Walker 1985, Riginos 2009, Cramer *et al.* 2010). When the average rainfall increases, grasses are less effective in limiting water availability to woody plants and therefore, more water is available to woody plants (Knoop and Walker 1985). The increased water availability to woody plants may provide woody plants with increased opportunities for recruitment and establishment. Therefore, increases in average rainfall may facilitate the encroachment of woody plants into savannas (Knoop and Walker 1985).

Recently, the increasing CO₂ levels associated with global warming have been proposed to be encouraging bush encroachment (Kgope *et al.* 2010, Ward 2010). A glasshouse test on the effects of elevated CO₂ levels on the C₃ savanna trees, *Acacia karroo* and *A. nilotica*, and the savanna C₄ grass, *Themeda triandra* was performed by Kgope *et al.* (2010). The tests demonstrated that along an increasing CO₂ concentration gradient, the photosynthesis, total stem length, total stem diameter, shoot dry weight and root dry weight increased significantly. For *T. triandra* however, there was no significant response to increased CO₂ levels (Kgope *et al.* 2010). Following the clipping of the trees, to simulate fire under increased CO₂ levels, tree recovery time was more rapid than at lower CO₂ levels. Therefore, at higher CO₂ levels woody plants may escape the effects of fire faster (by rapid growth) than they would at lower CO₂ levels (Kgope *et al.* 2010). Increased CO₂ levels may therefore reduce the effectiveness of fire in controlling bush encroachment in savannas (Kgope *et al.* 2010). We note that clipping may not effectively simulate fire (Hean and Ward, submitted). Furthermore, field studies have found little effect of increased CO₂ levels of tree:grass ratios (Körner *et al.* 2005, Stock *et al.* 2005). Therefore, the expected facilitation of woody plant encroachment by increased CO₂ must be applied cautiously to field experiments (Körner *et al.* 2005, Stock *et al.* 2005).

1.2. Aerial photographs

Textural analysis of woody vegetation using aerial photographs has been successful in assessing the historical changes in woody vegetation (Hudak and Wessman 1998, 2001). Importantly, image texture is based on the spatial variation in pixel intensities and is defined as the tonal variability in the spectral values of an image (Harralick *et al.* 1973). Image texture is a function of the fineness, coarseness,

contrast, regularity, directionality and periodicity in an image (Harralick *et al.* 1973). The properties that textural information provides have been used to assess bush density and cover (Hudak and Wessman 1998, 2001).

1.3. *The effects of fire in Ithala Game Reserve*

Ithala Game Reserve (IGR) in northern KwaZulu-Natal, South Africa, was proclaimed between 1972 and 1982 (Porter 1983). In IGR, concern has been raised about the number of woody plant species that are encroaching (Figure 1) (Porter 1983, Kotze 1990, Wiseman *et al.* 2004). Prior to the proclamation of IGR, the area was used for livestock farming and cropping in the flatter areas (Porter 1983, Wiseman *et al.* 2004). Fire has been of historical importance in IGR and was used by herdsman to provide nutritious regrowth of grasses for livestock and to control bush encroachment. Local people were observed to use fire frequently (annual to biennial burns) and patchily, to provide nutritious regrowth for livestock (Porter 1983). After the proclamation of IGR in 1972, a number of wild herbivores were reintroduced into the reserve. Fire was used as a tool by the conservation managers after the proclamation of IGR, particularly to control bush and manipulate the movement of grazing herbivores (Porter 1983, le Roux 1985).

This study uses aerial imagery to document and assess possible local (e.g. fire and herbivore numbers) and global drivers (e.g. rainfall patterns) of changes in woody vegetation cover and density changes in IGR. The following predictions are assessed in this study: (i) the density and cover of woody vegetation has increased since 1943 (the period for which aerial photographs are first available) to 1969 (the period just before the proclamation of IGR), (ii) the rate of woody vegetation increase has declined since the proclamation of IGR in 1972 to 2007 because of the negative impact of growing populations of different wild browsers on woody vegetation, (iii) areas in which fire has been suppressed (due to limited fuel loads) since the proclamation of IGR have had an increase in woody vegetation compared to areas where fire is frequent, and (iv) changes in rainfall patterns have facilitated bush encroachment. The identification of the factors influencing bush encroachment in IGR will allow a better understanding of how fire and herbivory may be used to control bush encroachment effectively.

2. Methods

2.1. Study site

Ithala Game Reserve (IGR) is located (27°30'S, 31°25'E) in northern KwaZulu-Natal, South Africa. The reserve covers 29 653 ha with the Pongolo River forming the northern boundary of the reserve. The altitudinal gradient of IGR corresponds to high variance in abiotic and biotic factors. Altitude ranges from 320 m a.s.l. at the Pongolo River, to 1 446 m a.s.l. on the southern escarpment plateau. The landscape types over this altitudinal gradient are complex ranging from plateaux, scarps, cliffs, deeply incised valleys and floodplains along the Pongolo River (van Rooyen and van Rooyen 2008). The geology of IGR comprises Archaean granite exposures, sandstones, shales and mudstones of the Karoo system and igneous dolerite dykes and sills. The soils are closely related to the geology, as many are formed *in situ* with underlying rocks. Granites generally form coarse-grained, nutrient poor soils. In contrast, dolerites and diabases produce fertile soils with poorer percolation than granite-derived soils (Hillel 1998, van Rooyen and van Rooyen 2008). The predominant soil type in the study area is shallow, rocky (lithosols) of the Mispah form (van Rooyen and van Rooyen 2008). IGR is a summer rainfall region, falling under the classification of a subtropical wet region (Benhin 2006), with a mean annual rainfall of 781 mm. Mean annual temperatures vary from 16.7 to 21.8°C and minimum and maximum temperatures range from 4.0 to 44.0°C, as measured from proximal areas (van Rooyen and van Rooyen 2008).

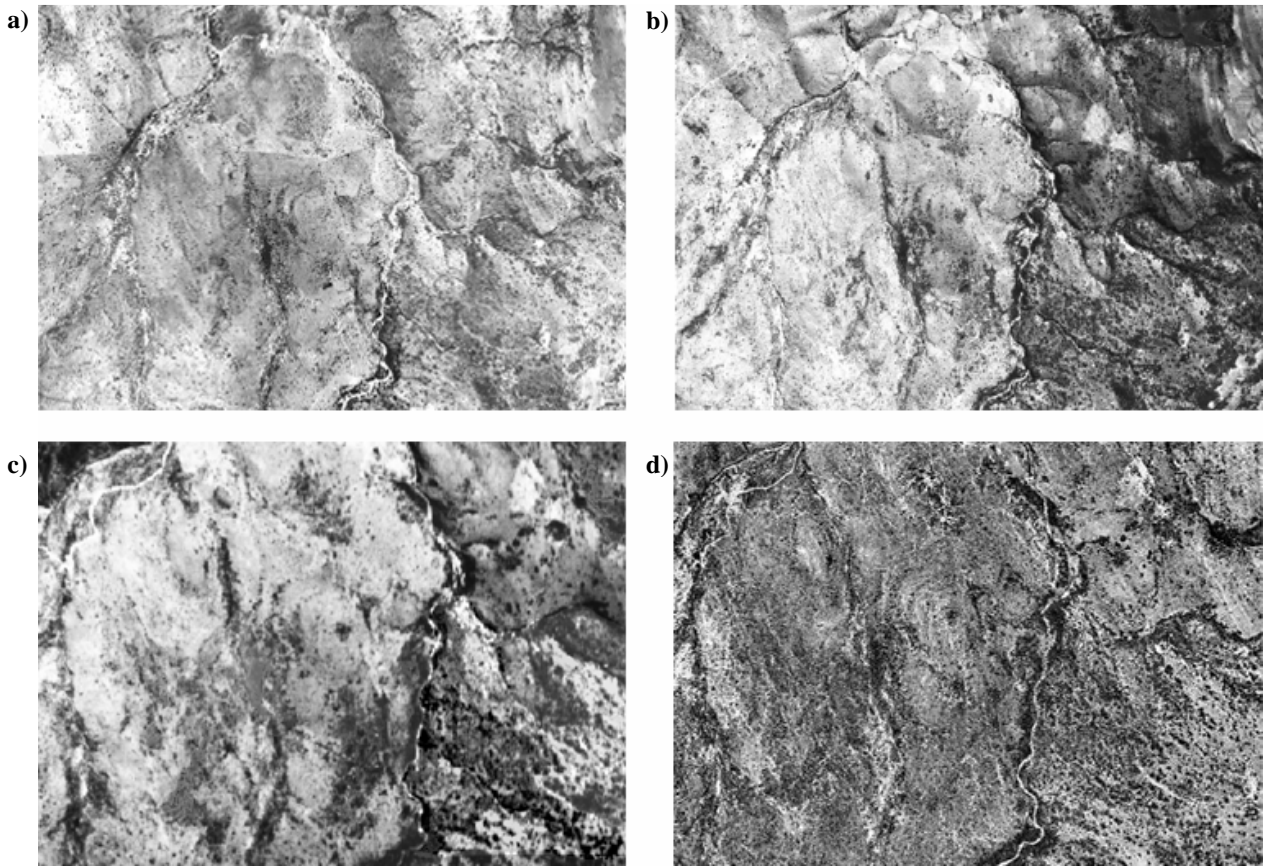


Figure 1: Georectified aerial photograph mosaics (scale: 1:22 000) from an area in Ithala Game Reserve, the Ngubhu basin. The sequence of images showing the same area, demonstrates bush encroachment from (a) 1943, (b) 1969, (c) 1990, and (d) 2007. The encroachment of woody plants from 1943 to 1969 appears to be less rapid than from 1990 to 2007. Emerging in the 1969 image, a few croplands are visible (small area with high reflectance/ contrasting patch of white). These croplands, hill shade (patches in the top-right hand corner of the 1969 image) and other burnt areas (e.g. dark area in the top-left hand corner and grey patches left of the 1990 image centre) were avoided for textural analysis. The high reflectance of the bare soil in the croplands/ old field grasslands, and the darkly burnt or shaded areas would have produced inaccurate estimates of woody vegetation cover and density.

2.2. Data acquisition and analysis

2.2.1. Rainfall data

Daily rainfall data from 1905 to 2009 was obtained from seven rainfall stations ranging within a proximity of 1–30km of IGR. The rainfall data was obtained from the Daily Rainfall Utility (Kunz 2004) and the South African Weather Service databases. The Standard Precipitation Index (SPI) has been successfully used to monitor drought and wet weather (Khan *et al.* 2008, Yurekli and Anli 2008). The continuous SPI measure is based on rainfall variability over the entire period of interest (Khan *et al.* 2008, Yurekli and Anli 2008). This index is calculated by dividing the difference in the normalised seasonal precipitation and its long-term seasonal mean by the standard deviation (see equation 1) (Yurekli and Anli 2008):

$$SPI = \frac{p_i - \sum_{i=1}^n \left(\frac{p_i}{n} \right)}{\sigma_p} \quad (1)$$

where *SPI* represents the standard precipitation index, p_i total annual rainfall for a given year, n the total length of record, and σ_p standard deviation. The SPI values describe rainfall variation ranging from extreme wet to extreme drought (Table 1) (Yurekli and Anli 2008). Significant changes in the frequency of rainfall events of given magnitudes (5 – 10mm, 10 – 20mm, 20 – 50mm and >50mm), from the 1st ten years to the last ten years of the period from 1910 to 2009, were tested using paired-sample *t*-tests.

Table 1: Standardized Precipitation Index classification

SPI Values	Classifications	SPI rank
>2.0	Extremely Wet	3
1.5 to 1.99	Very Wet	2
1.0 to 1.49	Moderately Wet	1
-0.99 to 0.99	Near Normal	0
-1.00 to -1.49	Moderate Drought	-1
-1.50 to -1.99	Severe Drought	-2
-2.0 and less	Extreme Drought	-3

2.2.2. Herbivore population estimates

In Ithala Game Reserve, indigenous animals were extirpated by the 1950s as a result of rinderpest and hunting (Wiseman *et al.* 2004). Cropping took place on the flatter areas of IGR. The grazing and browsing by mixed livestock was concentrated on the higher flatter portions of IGR, in the proximity of the old croplands (Porter 1983). From 1973 to 1987, 2 400 animals (representing 18 different species) were introduced into the reserve (le Roux 1987). These introductions included a number of megaherbivores, viz. black rhinoceros (*Diceros bicornis*), white rhinoceros (*Ceratotherium simum*), giraffe (*Giraffa camelopardis*) and elephant (*Loxodonta africana*).

Estimates of game were performed using aerial and ground-based census techniques in 2008, as described by van Rooyen and van Rooyen (2008). Since the elapse of time from 2007 (most recent time period assessed by this study) to 2008 was relatively short, the population estimates described by van Rooyen and van Rooyen (2008) were considered adequate for this study. The earlier estimates of a few species were given by Wiseman *et al.* (2004) (Table 2). A number of species such as impala *Aepyceros melampus* and particularly elephants *Loxodonta africana* (50 elephants were introduced in the period from 1990 to 1994) have had large increases in population sizes since the early 1990s (Wiseman *et al.* 2004). At first, wild animal numbers increased gradually from 1972 to 1985. From 1985 to the late 1990s, herbivore numbers increased exponentially, whereafter their numbers have stabilised (Wiseman *et al.* 2004, van Rooyen and van Rooyen 2008). Van Rooyen and van Rooyen (2008) calculated the recommended carrying capacity for the various herbivores based on the methods described by Bothma and van Rooyen (2004). A number of different species were in excess of the recommended (Bothma and van Rooyen 2004) browse and graze carrying capacities in 2008 (van Rooyen and van Rooyen 2008) (Table 2).

Table 2: Herbivore population estimates for IGR in 2008.

Species	1992 estimates	2000 estimates	Current Population	Recommended Population Size
Black Rhino (<i>Diceros bicornis</i>)	48	43	46*	42
Blue Wildebeest (<i>Connochaetes taurinus</i>)			1898*	1300
Buffalo (<i>Syncerus caffer</i>)			110	120
Burchell's Zebra (<i>Equus quagga burchellii</i>)			1675*	1500
Bushbuck (<i>Tragelaphus scriptus</i>)			50	50
Bush Pig (<i>Potamochoerus porcus</i>)			50	50
Common Reedbuck (<i>Redunca arundinum</i>)			89*	50
Eland (<i>Taurotragus oryx</i>)	123	124	27	50
Elephant (<i>Loxodonta Africana</i>)	30	56	130*	50
Giraffe (<i>Giraffa camelopardis</i>)	157	157	162*	90
Grey duiker (<i>Sylvicapra grimmia</i>)			50	50
Impala (<i>Aepyceros melampus</i>)	1243	1701	3915*	1600
Klipspringer (<i>Oreotragus oreotragus</i>)			50	50
Kudu (<i>Tragelaphus strepsiceros</i>)	498	750	810*	800
Mountain Reedbuck (<i>Redunca fulvorufula</i>)			185*	100
Nyala (<i>Tragelaphus angasii</i>)			250	250
Oribi (<i>Ourebia ourebi</i>)			20	20
Ostrich (<i>Struthio camelus</i>)			43	50
Red Hartebeest (<i>Alcelaphus caama</i>)			56	80
Steenbok (<i>Raphicerus campestris</i>)			20	20
Warthog (<i>Phacochoerus africanus</i>)			1319	1500
Waterbuck (<i>Kobus ellipsiprymnus</i>)			36	250
White Rhino (<i>Ceratotherium simum</i>)			43	50

* Indicates species whose population numbers are above recommended rates according to Bothma and van Rooyen (2004).

2.2.3. *The use of fire in Ithala Game Reserve*

The frequency of fire from the proclamation of the park to the early 1980s was calculated from Porter's (1983) fire frequency maps. Fire was used biennially in the savanna areas of IGR from 1972 to the late 1980s (le Roux 1985). In some areas of IGR, the frequency of fire has declined since the late 1980s. Notably, in part of the study area (Ngubhu basin (6820ha)), fire frequency declined from a biennial rate to zero fire frequency in the 2000s. The reason for the decline in fire frequency was because of insufficient fuel load accumulation (Wiseman *et al.* 2004, Ruinard 2009 pers. comm.). These areas with suppressed fire frequencies were compared to adjacent areas of similar topography with more frequent fires (>0.35 – 0.5 fires per annum from 1990 to 2007) in the textural analysis.

2.2.4. *Aerial imagery preparation*

High resolution (300dpi) aerial imagery was obtained from the Chief Director of Surveys and Land Information, Mowbray, South Africa. Three sets of aerial photographs were obtained from 1943, 1969 and 1990. Aerial photographs were taken using Wild RC cameras which absorb electromagnetic radiation in the visible colour spectrum (400 – 750nm). Aerial imagery from 2007 was also obtained from the Institute of Natural Resources, Pietermaritzburg, South Africa. The 2007 imagery had been orthorectified and was used as a base to georectify the images from 1943 to 1990. Unlike the earlier imagery, the 2007 aerial photographs were colour, not panchromatic. The 2007 imagery was comprised of three separate colour bands, blue, green and red. By combining (mean pixel values) the blue, green and red colour bands (between 400 – 750nm), the 2007 imagery was comparable to earlier panchromatic images, because of their common electromagnetic absorbance spectrum (400 – 750nm) (Wolf 1983, Lillesand and Kiefer 1987). All image histograms were radiometrically enhanced so that histograms were equalized within the 0-255 tonal value range (Hudak and Wessman 1998). This enabled a fair comparison of image tone (the standard 0-255 tonal value range) between different photographs (Hudak and Wessman 1998). In total, four sets of aerial images from 1943, 1969, 1990 and 2007 were used for change detection in woody vegetation. The scale and pixel sizes of the aerial images for the different time periods was 1:25 000 and 1.4m for 1943, 1:36 000 and 1.4m for 1969, 1:50 000 and 4.5m for 1990, and 1:30 000 and 1.4m for 2007.

The georectification of aerial photographs was performed using the spline transformation on ArcMAP version 9.3. The number of control points has been positively correlated with the accuracy of the spline transformation (Bangamwabo 2009). A minimum of 40 control points, evenly distributed on

each aerial photograph was selected to increase the accuracy of georectification (Bangamwabo 2009). Images were cropped so that the poor quality of photo edges was removed. The cropped images were joined to form a mosaic using ERDAS Imagine version 9.3.

2.2.5. *Detection of changes in woody vegetation and the response to fire suppression*

Due to the undulating nature of the topography in Ithala Game Reserve, the historical aerial photographs had high reflectance values in a number of areas (e.g. Figure 1). In addition, the bare soil of the old croplands had high reflectance values and visible contour lines. Therefore, the croplands were avoided for textural analysis because the high reflectance values of the old croplands would yield inaccurate results in a textural analysis (Hudak and Wessman 1998). Transects for textural analysis were evenly distributed within areas with none of the described high reflectance values produced by the bare soils of croplands. Burnt areas, steep hill slopes and valleys (hill shade) were also avoided to obtain accurate estimates of woody vegetation. The total area assessed using textural analysis was 134ha.

2.2.6. *Textural analysis*

Two classes of texture measures exist, first-order (occurrence) and second-order (co-occurrence) classes (Harralick *et al.* 1973). The first-order measure is designed to assess pixel intensities within a defined neighbourhood or a filter window. The second-order texture algorithms include spatial relationships between pixels. Due to their complexity and time-consuming processing, first order textural images are more frequently used. In this study, second-order texture images were used so that spatial textural information could be assessed and the representation of woody vegetation enhanced (Harralick *et al.* 1973). For woody vegetation studies it has been recommended that a 3×3 pixel filter window be employed (Moskal and Franklin 2002, Adjorlolo 2008). The 3×3 filter window allows the detection of individual trees' textural characteristics. We limited the size of trees to >1.8m canopy diameter as smaller trees could not be effectively detected with these images. Larger filter windows have undesirable smoothing effects on woody vegetation (Hudak and Wessman 1998, Moskal and Franklin 2002). As the pixel sizes of the imagery used in this study were all <4.5m, a <5×5m spatial representation of the ground sampling plots was acquired. This spatial representation has been shown to yield the most accurate results in quantifying woody vegetation cover and density (Hudak and Wessman 1998, 2001).

To create second-order textural images, algorithms are applied that assess spatial attributes of pixels. The algorithms of second-order textures assume that the probability of each pixel pair co-occur in a given direction and distance (Harralick *et al.* 1973). The combined conditional probabilities of co-occurring pixel values are then processed to produce textural values for the central pixel of a filter window (Harralick *et al.* 1973). The second order mean texture is calculated using the algorithms 2a and 2b:

$$\mu_i = \sum_{i,j=0}^{N-1} (p_{ij}) \quad (2a)$$

and

$$\mu_j = \sum_{i,j=0}^{N-1} j \cdot (p_{ij}) \quad (2b)$$

where μ_i and μ_j are the mean probability of pixel value co-occurrence, i and j the coordinates in the co-occurrence matrix, and p_{ij} the co-occurrence matrix value at the coordinates i, j . The mean, variance, contrast, homogeneity, entropy, correlation and second moment algorithms were used to calculate textural values (appendix 1). The remote sensing software ENVI 4.7 was used to calculate these textural measures.

2.2.7. Ground truthing and model validation

Woody plant transects were performed in the vegetation communities (mixed *Combretum – Acacia – Euclea* savanna) where textural analysis methods were applied. In each transect, the density and canopy dimensions, the longest and shortest orthogonal to estimate cover, of woody plants >1.0m were calculated. These measures have been correlated with the mean texture of aerial imagery (Hudak and Wessman 1998, 2001). To ground truth the remote sensing analysis, five transects were performed in open savanna, mixed and closed woodlands. In total, 15 transects (50m × 10m) were performed.

The mean texture values of the 2007 textural images were extracted from each of the 15 transects, using the Zonal Statistics tool in ArcMap version 9.3. To justify the use of image texture, the mean pixel intensity from non-textural images (unprocessed or raw images) were calculated for each of the 15 transects. To validate the relationship between the density and cover of woody vegetation and the mean textural and raw image values, simple linear regression was used. Simple linear regression models were produced to determine which types of textural measure (or raw image) (dependent variables) were best predicted by woody vegetation cover and density (Hudak and Wessman 1998). In

total, 16 simple linear models were produced. A sequential Bonferroni correction of α was applied to the p-values of the regression models to avoid a Type I error (i.e. spurious significant values from multiple tests of the same null hypothesis - Holm 1979). The significant model with the highest r^2 value was chosen to describe the relationship between mean textural (or raw image) values and woody vegetation density and cover. The testing of the normality and homoscedasticity of variance assumptions, and correlation and regression analyses were performed using SPSS version 15.0.

2.2.8. *Woody vegetation change*

The significant linear regression models were extrapolated to determine the canopy cover and density of woody plants (>1.0m in height) from textural images. In total, 336 50m×10m transects were used in the model extrapolation to assess changes in woody vegetation. The 336 transects were distributed in the same vegetation type where ground truthing was performed. This ensured the accuracy in the application of the linear regression models to calculate woody vegetation cover and density (Hudak and Wessman 1998). In total, 35 transects were randomly distributed in areas where fire was suppressed from ~1985 to 2007.

To standardize image tone between time periods, five control sites in open grasslands were selected (50m×10m) (Hudak and Wessman 2001). It was assumed that the vegetation at each of the control sites had remained unchanged. These were stable montane grasslands, as assessed for IGR by van Rooyen and van Rooyen (2008). To verify that the open savannas had remained unchanged, historic aerial photographs were visually compared with 2007 aerial photographs. The density and cover of woody plants were also measured in these five control transects in 2007. At each of these sites, the mean pixel values of the textural images were calculated for 1943, 1969, 1990 and 2007. The difference between the mean texture of the five control sites in the 2007 textural image and each previous year (1943, 1969 and 1990), was used as the control for each respective year, following Hudak and Wessman (2001) (see equations 3 – 5):

$$K_{2007-1943} = CST_{(2007)} - CST_{(1943)} \quad (3)$$

$$K_{2007-1969} = CST_{(2007)} - CST_{(1969)} \quad (4)$$

$$K_{2007-1990} = CST_{(2007)} - CST_{(1990)} \quad (5)$$

where K_{x-y} is the mean texture adjustment factor from year x to year y , and $CST_{(z)}$ is the mean control site texture for year z (Hudak and Wessman 2001).

The changes in the mean woody vegetation cover and density were assessed between each period and: before the proclamation of IGR in 1972 (from 1943 to 1969) and after the proclamation of IGR from 1969 to 2007, using a one-way ANOVA with Scheffe *post hoc* tests. After the proclamation of IGR, the differences in the increases (from recent to earlier periods) in woody vegetation cover and density between areas that experienced fire suppression (Ngubhu basin area, southwestern 17% of IGR) and frequent fires were assessed using one-way ANOVAs with Scheffe *post hoc* tests. These statistical tests and assumptions of normality and homoscedasticity were performed on SPSS version 15.0. Box-Cox transformations were applied to the cover and density data so that the assumption of normality was verified (Box and Cox 1962). Box-Cox transformations are computed as shown in equations (6) and (7):

$$X' = \frac{x^\lambda - 1}{\lambda} \quad (\text{when } \lambda \neq 0) \quad (6)$$

or

$$X' = \log X \quad (\text{when } \lambda = 0) \quad (7)$$

where X' is the transformed value and λ is the value calculated to transform data to a normal distribution (Krebs 1989).

3. Results

3.1. Rainfall patterns

The period from 1910 to 1943 was characterized by two seasons of extreme drought in 1926 and 1927 (Figure 2). A severe drought, moderate drought and extremely wet season also occurred during this period. From 1943 to 1969, two moderate droughts and one extreme drought occurred. There were also three moderately wet seasons in this period. From 1969 to 1990, there were 2 moderate drought and wet seasons and one very wet and severe drought season. In addition, there was an extremely wet season in 1984. The period from 1990 to 2007 is characterized by relatively more wet seasons than earlier periods. The frequency of high magnitude (20 – 50mm, >50mm) rainfall events increased

significantly from the 1st ten years to the last ten years of 1910 to 2009, by ~three to ~ten events (20 – 50mm: $t_9 = 4.47$, $p_{0.05} < 0.001$; >50mm: $t_9 = 4.49$, $p_{0.05} < 0.001$). The frequency of light rainfall events (5 – 10mm) decreased by ~30 days, from the 1st ten years to the last ten years of 1910 to 2009 ($t_9 = 6.12$, $p_{0.05} < 0.001$) (Figure 3). The difference in number of rainfall events of the magnitude 10 – 20mm, from the 1st ten years to the last ten years of the period from 1910 to 2009 was non-significant ($t_9 = 0.594$, $p_{0.05} = 0.954$).

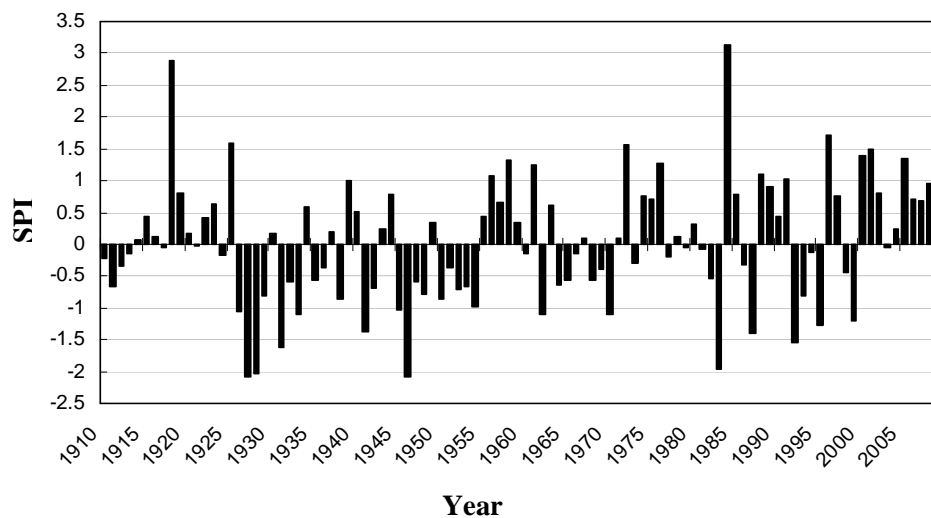


Figure 2: The relative amount of precipitation in each season (SPI) from 1910 to 2009 (see Methods). SPI values indicate the relative amount of precipitation in each season and are ranked into several categories (Table 1).

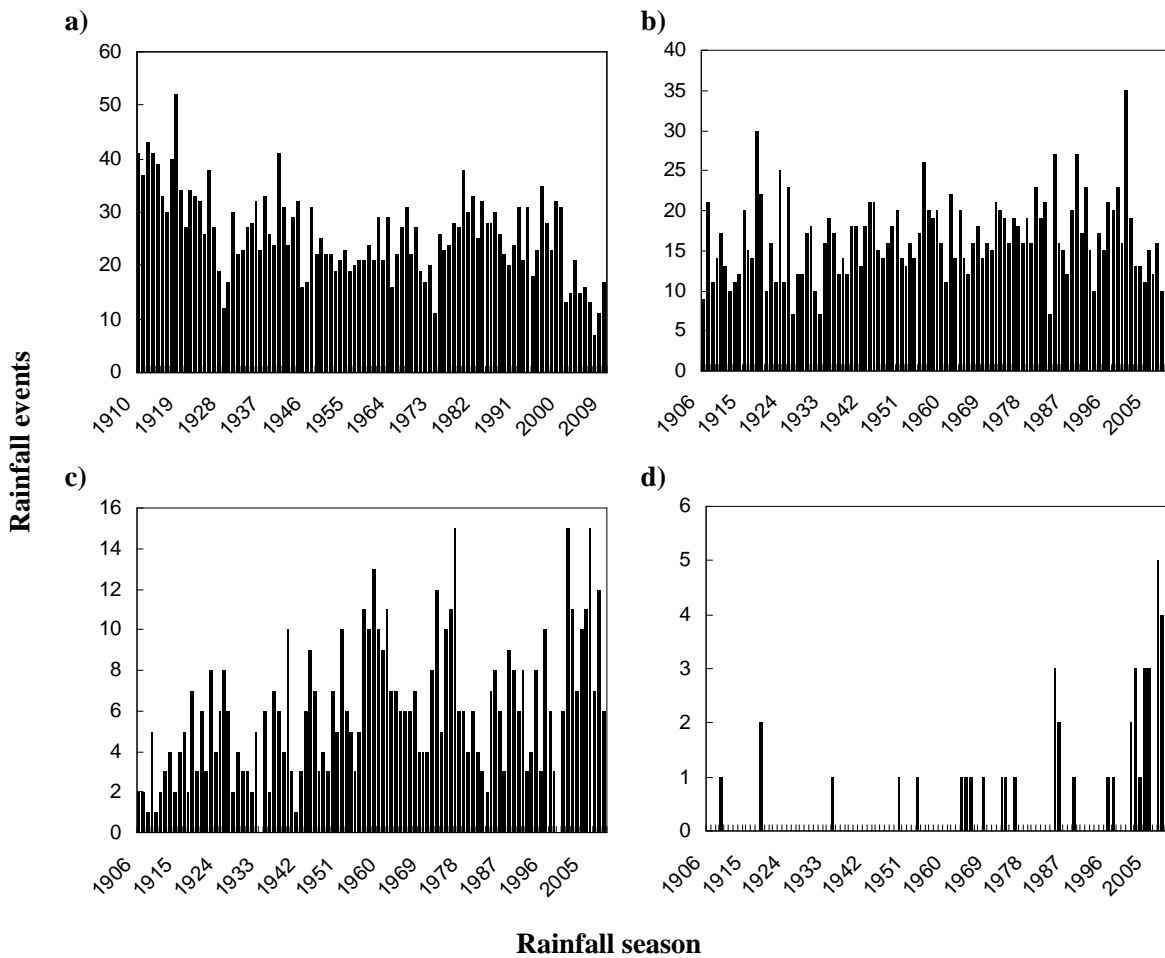


Figure 3: The number of rainfall events of magnitude (a) 5 – 10mm, (b) 10 – 20mm, (c) 20 – 50mm and (d) >50mm per rainfall season from 1910 to 2009.

3.2. Ground truthing and model validation

The regression analyses revealed that the mean co-occurrence textural image and the raw, unprocessed image were significantly correlated with the percentage cover of woody plants (Table 3). The density of woody individuals was also significantly correlated with the mean co-occurrence textural band and raw image.

Table 3: Correlations between the co-occurrence textural images and the “raw” pixel values for the 2007 aerial photography and the density (woody individuals >1m high per ha), mean canopy length (m), and % canopy cover. (Note: the second moment is a measure of homogeneity, entropy describes spatial uncertainty, and contrast describes the local variation of pixel values (Yuan *et al.* 1991). The different texture measures are further described with their algorithms in Appendix 1).

		Second			
		Moment	Contrast	Correlation	Entropy
Density	Pearson				
	Correlation (r)	-0.629†	0.569†	0.539†	0.554†
	p value	0.012	0.027	0.038	0.032
Percentage cover	Pearson				
	Correlation (r)	-0.596†	0.439	0.488	0.513
	p value	0.019	0.101	0.065	0.051
		Homogeneity	Mean	Variance	Raw
Density	Pearson				
	Correlation (r)	-0.583†	-0.714‡	0.532†	-0.686‡
	p value	0.022	0.003	0.041	0.005
Percentage cover	Pearson				
	Correlation (r)	-0.540†	-0.891‡	0.421	-0.877‡
	p value	0.038	0.000	0.118	0.000

‡ Correlation is significant at the 0.01 level (2-tailed).

† Correlation is significant at the 0.05 level (2-tailed).

The sequential Bonferroni adjustment of α indicated that both simple linear regression models for the cover ($F_{1, 14} = 13.51$, $p_{0.05} = 0.003$) and density ($F_{1, 13} = 22.59$, $p_{0.05} < 0.004$) of woody vegetation (ground-truthed data) significantly predicted the *mean* textural image. These models describing the relationship between the cover ($r^2 = 0.71$) and density ($r^2 = 0.64$) of woody vegetation and the mean textural image had the highest r^2 values. The constant parameters for the regression analyses were also significant for canopy cover ($t = 8.810$, $p_{0.05} < 0.001$, error d.f. = 14) and density ($t = 5.184$, $p_{0.05} < 0.001$, error d.f. = 14) of woody plants (Figure 4).

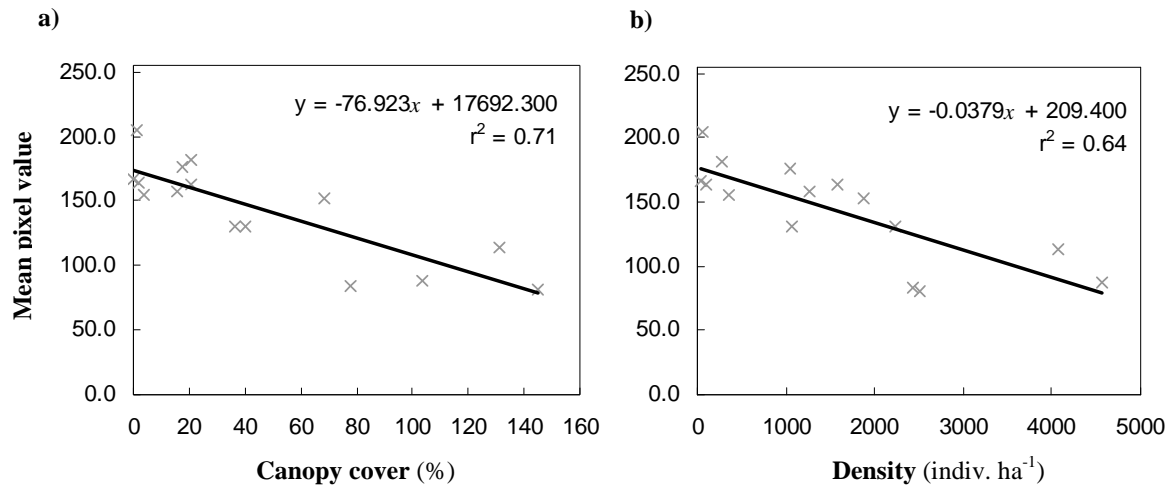


Figure 4: Linear regression models depicting the relationship between (a) percentage cover, and (b) density of woody individuals (>1.0m in height) and the mean pixel values of the mean co-occurrence textural band in the 0 – 255 tonal value range (Hudak and Wessman 1998). The equations and r^2 values describing the linear relationships are displayed next to each regression line. Note that the canopy cover estimates were derived from the canopy dimensions of woody plants. Therefore, the overlap of tree canopies allowed cover estimates that exceed 100% in some transects.

3.3. Woody vegetation change

There were significant increases in the mean cover and density of woody vegetation between the years 1943, 1969 and 2007 (cover: $F_{2, 249} = 47.78$, $p_{0.05} < 0.001$; density: $F_{2, 249} = 35.53$, $p_{0.05} < 0.001$). The overall mean \pm S.E. increase in woody vegetation cover and density over 64 years was $32.5\% \pm 3.96\%$ and 657.9 ± 80.24 indiv. ha⁻¹, respectively. The mean \pm S.E. increase in woody vegetation cover ($0.03 \pm 0.017\%$) and density (53.9 ± 34.62 indiv. ha⁻¹) from 1943 to just before the proclamation of IGR in 1969, was however non-significant (cover: $p_{0.05} = 0.541$; density: $p_{0.05} = 0.690$).

After the proclamation of IGR, from 1969 to 2007, the mean \pm S.E. increase in woody vegetation cover ($29.8 \pm 4.40\%$) and density (604.1 ± 89.03 indiv. ha⁻¹) was significant (cover: $p_{0.05} < 0.001$; density: $p_{0.05} < 0.001$). In areas where fire was suppressed, following the proclamation of IGR, the increase in mean woody vegetation cover and density was significantly greater than in areas where fire was used frequently (cover: $F_{3, 158} = 8.24$, $p_{0.05} < 0.001$; density: $F_{3, 161} = 7.84$, $p_{0.05} < 0.001$) (see Table 4 for Scheffe *post hoc* test results).

Table 4: Mean differences in woody vegetation canopy cover and density between areas where fire was suppressed (biennial to zero fire frequency from mid-1985 to 2007) and where fire was used frequently (~biennial fire frequency), over the different time periods assessed since the proclamation of IGR in 1972. We subtracted the values for a particular year from the previous year's value (e.g. 1990-1969). Significantly greater increases in the density and mean cover (Box-Cox transformed data) of areas where fire was suppressed were calculated using Scheffe *post hoc* tests and are formatted in bold.

	Canopy cover (%)	Density (indiv. ha⁻¹)
1990 – 1969	4.8	97.6
2007 – 1969	21.3†	431.9†
2007 – 1990	16.5†	334.4†

† Difference is significant at the 0.05 level.

The significant mean increase in the cover and density of woody vegetation from 1990 to 2007 was greater and more rapid in areas with suppressed fire frequencies (due to low fuel loads) than in areas with frequent fires (>16.5% in canopy cover and >334.4 indiv. ha⁻¹ in density) (Table 4 and Figure 5).

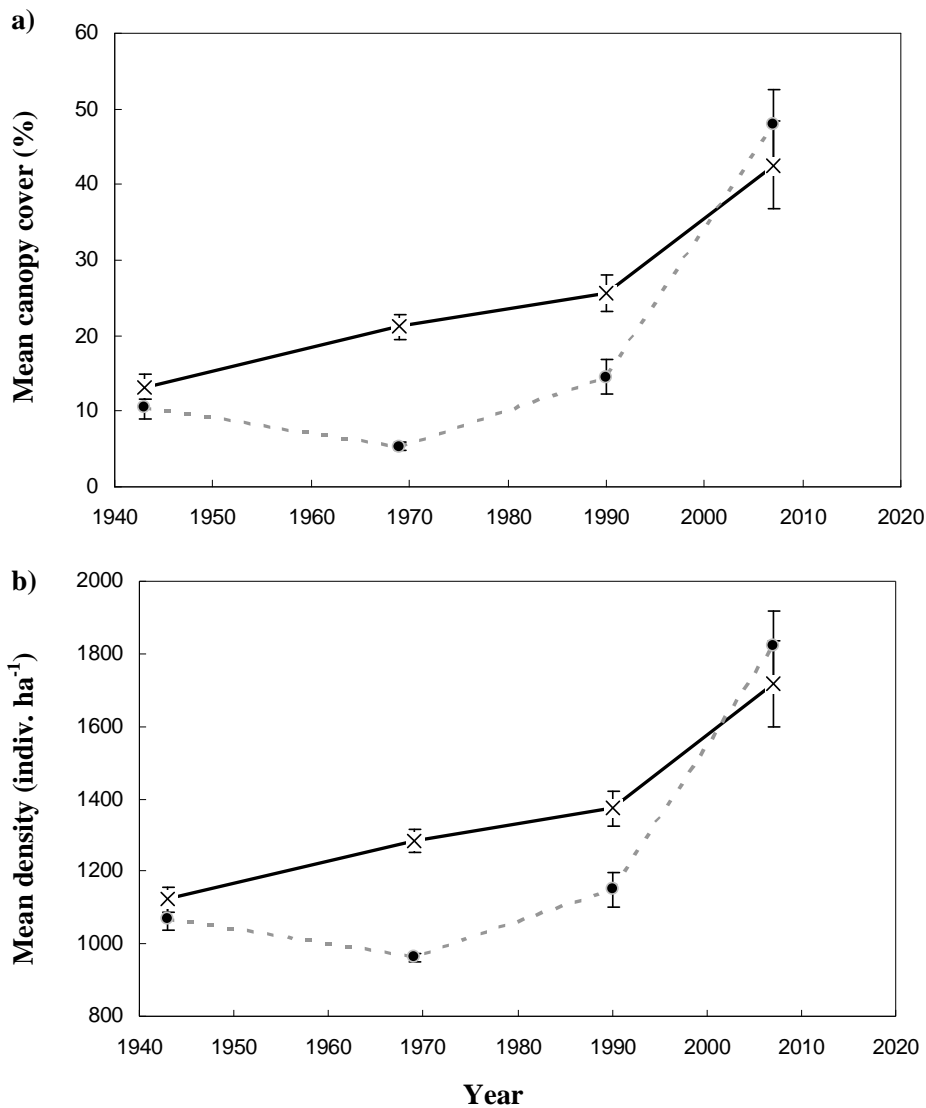


Figure 5: Estimated mean change in woody vegetation (a) cover and (b) density from the year 1943 to 2007. The dashed lines represent areas (the Ngubhu basin) that experienced a decrease in fire frequency (from biennial to zero fire frequency) from 1985 to 2007. Solid lines represent areas where fire has occurred frequently (~biennial). Error bars represent ± 1 S.E.

4. Discussion

Similar increases in woody vegetation, as those documented in Ithala Game Reserve in this study, have been observed elsewhere. In mesic savannas surrounding IGR, Roques *et al.* (2001) and Wigley *et al.* (2010) reported increases of 29 and 44%, over 43 and 67 years, respectively. Roques *et al.* (2001) determined that the fire-grazing relationship was important in controlling bush encroachment. Light grazing allowed the accumulation of fuel or grassy biomass for burning frequently. This frequent burning was important in suppressing bush encroachment (Roques *et al.* 2001). Drought was another important factor that in combination with light grazing and frequent fires was observed by Roques *et al.* (2001) to reverse bush encroachment. Wigley *et al.* (2010) acknowledged local drivers, such as fire and grazing, as possible causes of bush encroachment. However, they suggested that increasing CO₂ levels was the main cause of the bush encroachment they observed (Wigley *et al.* 2010).

The land use practices in IGR prior to its proclamation may have had a controlling effect on bush encroachment (Figure 5). The extensive harvesting of trees for fire wood and as construction materials may have hindered the rate of tree encroachment (Porter 1983). In addition, the long dry period from 1925 to 1971 in IGR, that included a number of severe and extreme droughts, frequent fires, and browsing by goats (Hester *et al.* 2006) may have decreased the rate of bush encroachment in IGR relative to other areas (Figure 2) (Mueller *et al.* 2005, Gignoux *et al.* 2009).

Despite the reduction in bush encroachment facilitated by humans, drought, fire and goat browsing prior to 1972, there was a mean increase in woody vegetation over time. A number of factors were identified that facilitated this overall increase in woody vegetation in IGR. The increase in rainfall magnitude from 1910 – 2010, may have played a role in the increase of woody vegetation in IGR. The frequency of higher magnitude rainfall events (>20mm) increased from 1910 to 2007 (Figure 3). In contrast, the frequency of rainfall events of lesser magnitude (5 – 10mm) decreased over this period. Similar changes in rainfall patterns have been documented for other areas in the subtropical wet rainfall regions of South Africa (Smakhtina 1998, Benhin 2006). These changes in rainfall patterns over the 20th century may be enhancing the competitive ability of woody plants relative to grassy plants (Knoop and Walker 1985). Grasses are known to respond rapidly to resource pulses (Chesson *et al.* 2004). This ability may restrict woody plant access to water in shallow and subsoil layers (Walter 1939, Knoop and Walker 1985, Bond 2008). When the magnitude of a rainfall event is above the average threshold, grasses become limited in the amount of water they can absorb from the

soil. The water they cannot absorb is therefore available to woody plants (Knoop and Walker 1985). Therefore, with the increase in rainfall magnitude over the 20th century, woody plants have been benefiting from increased water availability (Knoop and Walker 1985).

Fire was found to have an important controlling effect on woody vegetation. After the proclamation of IGR from 1972 to 2007, in areas where fire frequency was suppressed, the overall increase in woody vegetation cover and density was significantly greater than in areas where fire was used frequently (Table 4 and Figure 5). This observation corresponds to the observations of Skowno *et al.* (1999) in a nearby savanna in Hluhluwe Game Reserve. Following the suppression of fire, they observed a rapid increase in woody vegetation cover (Skowno *et al.* 1999). Similarly, in this study, the rapid invasion of woody plants occurred within about a decade after fire suppression. This confirms the importance of fire in controlling woody vegetation in mesic savannas (>650mm annual rainfall (Sankaran *et al.* 2005)) (Skowno *et al.* 1999, Bond and Archibald 2003, Fynn *et al.* 2005).

The role of herbivory cannot be ignored (Midgley *et al.* 2010). Fire and herbivory have been described to act synergistically (Midgley *et al.* 2010). To fuel hot fires to control tree encroachment, sufficient fuel in the form of grass is required (van Langevelde *et al.* 2003). Grazing herbivores consume grassy biomass and may therefore limit the frequency and intensity of fires (van Langevelde *et al.* 2003). Therefore, grazing herbivores, through their influence on fuel accumulation, played an important role in bush encroachment. Most notably, grazers limited the accumulation of the fuel load and decreased the intensity and frequency of fires in some areas (Wiseman *et al.* 2004). This decrease in fire frequency and intensity allowed the rapid encroachment of woody plants from 2000 to 2007 in some areas of IGR.

After the proclamation of IGR, the increase in wild browsing herbivores has been evident in the woody vegetation dynamics. From 1990 to 2000, Wiseman *et al.* (2004) using field data documented a decline in the density of woody plants in IGR. The decrease in the density of woody individuals was associated with a decline in deciduous microphyllous palatable species (such as *Acacia nilotica* and *A. gerrardii*). These palatable species were observed by Wiseman *et al.* (2004) to decrease from 1990 to 2000, and from 2000 to 2009 by Rice (2010). In contrast however, unpalatable evergreen macrophyllous woody species such as *Euclea* and *Searsia* (formerly *Rhus*) species were observed to increase from 1990 to 2010 (Wiseman *et al.* 2004, Rice 2010). This suggests that browsing herbivores may have played a role in the change in density and composition of woody vegetation in IGR (Wiseman *et al.* 2004).

Although there was an overall increase in woody vegetation from 1972 to 2007, as indicated by the textural analysis, field studies indicated that the density of woody plants in the Ngubhu basin (southwestern 17% of IGR) decreased from 1990 to 2000 (Wiseman *et al.* 2004). It appears that browsers along with fire facilitated the reduction in the density of woody plants from 1990 to 2000, as indicated by Wiseman *et al.* (2004). From 2000 to 2009 however, a repeat study documented an increase in the density of woody vegetation (Rice 2010). In the Ngubhu area of IGR, which had a decrease in fire frequency from a biennial rate, prior to 1985, to a zero fire frequency rate from 2000 to 2007, the density of woody plants (>0.7cm stem diameter), increased from 4 136 to 22 323 indiv. ha⁻¹ (Wiseman *et al.* 2004, Rice 2010). This rapid invasion of woody plants corresponds to the large increase in woody vegetation observed in the textural analysis from 1990 to 2007. Therefore, the prediction that after the proclamation of IGR, from 1972 to 2007, the increasing biomass of browsers would result in a decrease in woody vegetation density was incorrect.

The fact that the palatable microphyllous woody species have been replaced by unpalatable macrophyllous woody species has prevented browsers from controlling woody plant encroachment in IGR. The increase in unpalatable macrophyllous species, as a result of their release from herbivory, has allowed their proliferation and the formation of macrophyllous thickets (Wiseman *et al.* 2004, Rice 2010). Furthermore, the proliferation of these unpalatable woody plants may be suppressing the herbaceous layer through a reduction in light availability (van Langevelde *et al.* 2003). In addition to the suppression of the herbaceous layer by the increase in macrophyllous thickets, the increases in grazing herbivores have also reduced the fuel load accumulation in IGR. This suppression of the herbaceous layer has resulted in decreased fire intensities and frequencies (Wiseman *et al.* 2004). Thus, this fire suppression has facilitated the rapid increase of woody vegetation in the Ngubhu basin area of IGR.

Through direct and indirect impacts (trampling, grass consumption and seed dispersal), grazing and browsing herbivores have been known to positively influence woody plant germination and establishment (e.g. Danell *et al.* 2006). This was particularly true in IGR from 2000 to 2009 when the density of woody plants increased from 4 136 to 22 323 indiv. ha⁻¹, with the increase in both grazing and browsing herbivore populations from the mid 1980s to the late 1990s (Wiseman *et al.* 2004, van Rooyen and van Rooyen 2008). Herbivores have therefore played an important role in the regulation of IGR's fire regimes and the increase in bush densities. Furthermore, the temporally and spatially stochastic nature of rainfall (see Figure 1) may introduce further variability in grassy biomass

accumulation and herbivore movements, which ultimately affects fire intensities and its effects on woody plant densities (Balfour and Howison 2002). Future studies need to focus on the effects of grazing on fuel load accumulation by studying piospheres or herbivore exclusion plots.

5. Conclusions

This study confirmed the prediction that woody vegetation cover and density has increased from 1943 to 2007 in Ithala Game Reserve. A number of local and global drivers of woody vegetation change were identified. Locally, the increase in woody vegetation cover and density was associated with livestock farming, from 1884 to 1972 (Porter 1983). However, after the proclamation of IGR in 1972, despite the large increase in browser biomass, the rate of woody vegetation encroachment accelerated. In particular, a rapid increase in woody vegetation was observed in areas where fire was suppressed from 2000 to 2007. This confirms the prediction that the suppression of fire would result in an increase in woody vegetation encroachment. Furthermore, it appears that the roles of grazing and browsing herbivores may have acted in tandem with the role of fire.

After the proclamation of IGR, the spatial variation in herbivore impacts and the consequential change in fire regimes played a role in the increase in woody vegetation. Despite the overall increase in woody vegetation, browsers and fire facilitated an initial decrease in the density of woody vegetation from 1990 to 2000 (Wiseman *et al.* 2004). This decline in the density of woody plants was concomitant with a reduction in palatable species (such as *Acacia nilotica* and *A. gerrardii*) and an increase in unpalatable species (such as *Euclea* and *Searsia* spp.) (Wiseman *et al.* 2004, Rice 2010). For effective control of bush encroachment in IGR, it appears that fire and the appropriate numbers and ratios of grazing and browsing herbivores have to be achieved. It should be noted that heavy grazing and browsing may reduce the effectiveness of fire in controlling bush encroachment.

Globally, the change in rainfall patterns associated with climate change (Smakhtina 1998, Benhin 2006) may explain part of the increase of woody vegetation in IGR. The observed increase of rainfall events >20mm, and the concomitant reduction of rainfall events 5 – 10mm, may have enhanced the competitive ability of woody plants against grassy plants (Knoop and Walker 1985). The dry period with a number of droughts from 1926 to 1972, and browsing by goats may have limited tree

densities despite the increased grazing, which has been associated with bush encroachment (e.g. Walter 1939, Roques *et al.* 2001).

Climate change has also been hypothesized to increase the competitive ability of trees against grasses with increasing CO₂ levels (Polley *et al.* 1997, Bond *et al.* 2003, Ward 2010). This may explain part of the cause of the observed increase in woody vegetation (Ward 2010). However, the mechanisms described above (i.e. excluding increases in CO₂ levels but including rainfall changes) explain much of the increases in woody vegetation in IGR.

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Appendix 1:

Table 1: Algorithms used to calculate different measures of co-occurrence texture used in this study. Formulas are given where μ_i and μ_j are the mean probability of pixel value co-occurrence, i and j the coordinates in the co-occurrence matrix, σ is the variance of pixel values in a matrix, and p_{ij} the co-occurrence matrix value at the coordinates i, j . A brief description of each measure is given.

Co-occurrence	Formula	Description
Textural measure		
Homogeneity	$\sum_{i,j=0}^{N-1} \frac{P_{i,j}}{1+(i-j)^2}$	Calculates the smoothness of an image (Tuttle <i>et al.</i> 2006).
Second Moment	$\sum_{i,j=0}^{N-1} P_{i,j}^2$	A measure of homogeneity (Yuan <i>et al.</i> 1991).
Entropy	$\sum_{i,j=0}^{N-1} P_{i,j} (-\ln P_{i,j})$	A statistical measure of uncertainty (Yuan <i>et al.</i> 1991).
Mean	$\mu_i = \sum_{i,j=0}^{N-1} i(P_{i,j})$ $\mu_j = \sum_{i,j=0}^{N-1} j(P_{i,j})$	Mean probability of the co-occurrence of a pixel value (Lévesque and King 2003).
Variance	$\sigma_i^2 = \sum_{i,j=0}^{N-1} P_{i,j} (i - \mu_i)^2$ $\sigma_j^2 = \sum_{i,j=0}^{N-1} P_{i,j} (j - \mu_j)^2$	Describes the variability of the spectral response of pixels (Lévesque and King 2003).
Correlation	$\sum_{i,j=0}^{N-1} P_{i,j} \cdot \left[\frac{(i - \mu_i)(j - \mu_j)}{\sqrt{(\sigma_i^2)(\sigma_j^2)}} \right]$	Calculates the pixel values linear-dependency within the image (Kayitakire <i>et al.</i> 2006).
Contrast	$\sum_{i,j=0}^{N-1} P_{i,j} (i - j)^2$	A measure of local variation within a window (Yuan <i>et al.</i> 1991).

Chapter 3:

Fire suppresses the development of macrophyllous thickets in Ithala Game Reserve

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Abstract

The ingression of woody plants into savannas, known as bush- or shrub- encroachment, has become a global concern. Fire has been acknowledged as a key factor in managing woody vegetation in savannas. The suppression of fire has been reported to result in the conversion of savannas into closed woodlands/ macrophyllous thickets within a decade. Recently however, despite the frequent use of fire, its pivotal role has been questioned. This study assessed the role of fire in determining the total density, structure and composition of woody vegetation in Ithala Game Reserve. To achieve this, we surveyed woody vegetation in comparable areas with different fire frequencies. In *Combretum* woodlands, there was no significant effect of fire frequency on the total density of woody individuals. In old field grasslands, the density of woody plants was greater in areas burnt annually and in areas burnt once every ten years, compared to areas burnt once every 2 to 4 years. In these grasslands, areas burnt annually were dominated by woody plants <2m in height. Herbivore and fire interactions may explain these results. Multivariate analyses also indicated a significant effect of fire frequency on woody vegetation composition. To control encroaching trees such as *Dichrostachys cinerea* and *Acacia karroo*, and the development of macrophyllous thickets, an intermediate fire frequency is required (one burn every 2 to 4 years).

Keywords: Bush encroachment, *Acacia karroo*, *Dichrostachys cinerea*, microphyllous and macrophyllous vegetation.

Introduction

Bush encroachment or the ingression of woody plants into grasslands and savannas has become a global concern (Bond 2008). Typically, unique rainfall conditions, heavy grazing and the suppression of fire have been considered to cause bush encroachment (Ward 2005). More recently, the increasing CO₂ levels associated with global warming have been hypothesized to enhance the ability of woody species to encroach (Polley *et al.* 1997, Bond and Midgley 2000, Kgope 2010, Ward 2010).

Fire has been described as a principal tool for managing rangelands (Trollope and Tainton 1986, Bond and Archibald 2003, Hudak and Fairbanks 2004). In particular, fire has been considered an important agent in the control and determination of savanna woody vegetation structure and composition (Higgins *et al.* 2000, Bond and Archibald 2003, Hoffmann *et al.* 2003, Sankaran *et al.* 2008). Many savannas contain patches of evergreen macrophyllous (or broad-leaved) woody plants, dispersed within a matrix of deciduous microphyllous (fine-leaved) woody species (Hoffmann *et al.* 2003, Gignoux *et al.* 2009). Compared to microphyllous woody species, these macrophyllous woody species are more susceptible to fire-induced mortality, due to their comparatively thinner insulating layer of bark (Hoffmann *et al.* 2003). However, the clustering of these evergreen macrophyllous species results in fire-resistant thickets (due to their typically less flammable leaves) (Hoffmann *et al.* 2003, Gignoux *et al.* 2009). The understory of dense macrophyllous thickets are also more humid than microphyllous savannas and may shade out grasses, adding to their resistance to fire and longevity (Skowno *et al.* 1999, Hoffmann *et al.* 2003, Gignoux *et al.* 2009). Fire has played an important role in preventing the expansion and formation of macrophyllous thickets (Skowno *et al.* 1999, Hoffmann *et al.* 2003, Bond and Keeley 2005, Gignoux *et al.* 2009).

The encroachment of savannas by deciduous microphyllous woody species (e.g. *Acacia spp.* and *Dichrostachys cinerea*) may precede and facilitate the development of macrophyllous woody thickets. Increased densities of woody plants may suppress the herbaceous layer, resulting in lower fire frequencies (van Langevelde *et al.* 2003). The reduction in fire frequencies would therefore allow the proliferation of pyrophobic macrophyllous trees, and lead to the development of macrophyllous thickets (Skowno *et al.* 1999). This trend of increasing macrophyllous woody vegetation following the suppression of fire has been observed in many areas (Bowman and Fensham 1991, Hopkins 1992, Swaine *et al.* 1992, King *et al.* 1997). Remarkably, the release from fire in some areas has led to the conversion of savanna to macrophyllous thickets within a decade (Skowno *et al.* 1999, Bond and

Archibald 2003). Recently however, the role and ability of fire in controlling woody vegetation in savannas has been questioned (Higgins *et al.* 2007, Balfour and Midgley 2008).

In some savannas, fire has been shown to be effective in controlling the density of woody plants (Hoffmann 1999, Higgins *et al.* 2007). However, in other savannas, fire has had no effect on the density of woody plants (Higgins *et al.* 2007). More particularly, the role of fire in controlling deciduous microphyllous woody species has been questioned (Higgins *et al.* 2007, Wakeling and Bond 2007). Apart from the density of woody plants, woody vegetation structure has also been shown to be influenced by fire (Higgins *et al.* 2000, Higgins *et al.* 2007). Higgins *et al.* (2000) described the effects of fire on savanna woody plants using the framework of the “storage effect” (Warner and Chesson 1985). For the storage effect to work, the longevity of mature woody plants in savannas is important because recruitment is considered to be limited. Long-lived mature individuals in the population are required to produce seed (Bond and van Wilgen 1996). Seeds then germinate during favourable conditions that are temporally stochastic, for example during periods of high rainfall frequency (Wiegand *et al.* 2004, Ward 2005). Once germinated, establishment occurs under favourable environmental conditions, however disturbance factors and competitive interactions generally suppress the growth of establishing woody plants (Ward 2005).

The “fire trap” describes the disturbance zone <4m high, within which establishing woody plants are limited by fire (Trollope and Tainton 1986). Fire limits the growth of these shorter woody plants by inducing above-ground stem death or topkill (Trollope and Tainton 1986, Balfour and Midgley 2006). Frequent fires therefore limit the recruitment of these woody plants “caught” within the “fire trap” (Bond and van Wilgen 1996, Higgins *et al.* 2000). These woody plants within the “fire trap” have been described as “gullivers,” suppressed by “lilliputian” grasses that fuel fires (Bond and van Wilgen 1996, Bond and Midgley 2000). To survive frequent disturbances, woody plants within the “fire trap” have to be able to resprout and compete with grasses for moisture and nutrients (Knoop and Walker 1985, Higgins *et al.* 2000, Riginos 2009). The woody plants that survive as “gullivers” within the “fire trap” may escape the recruitment bottleneck by growing taller during favourable periods (e.g. during the release from fire) (Bond and van Wilgen 1996, Higgins *et al.* 2000). Once mature, these individuals are able to produce seed and contribute to the storage effect by virtue of their longevity (Higgins *et al.* 2000).

Similarly to fire, browsing may reduce the height of woody plants (Pellew 1983, Higgins *et al.* 2000). Unlike fire though, browsers show dietary preferences and avoid woody plants that have poor

nutritional value (Cooper and Owen-Smith 1985, Cooper *et al.* 1988). For example, many plants contain tannin compounds that inhibit protein digestion, therefore lowering the relative amount of available protein. Therefore, plants with high tannin:protein ratios would be avoided by herbivores and are termed unpalatable (Cooper and Owen-Smith 1985, Cooper *et al.* 1988). The browsing by herbivores may have important implications for woody vegetation structure and composition (Cooper and Owen-Smith 1985, Cooper *et al.* 1988). Particularly, browsers and fire working together reduce the density of woody plants in savannas (Wiseman *et al.* 2004, Midgley *et al.* 2010).

The encroachment of woody plants in Ithala Game Reserve (IGR), in northern KwaZulu-Natal, South Africa, despite the use of fire calls into question the effectiveness of the historical fire regime. This study aims to assess the role of fire in woody vegetation encroachment in IGR. The following predictions were tested in this study: (i) areas with a higher fire frequency (FF) have a decreased density of woody plants compared to areas burnt less frequently (Hoffmann 1999), (ii) areas with higher FFs have increased densities of shorter woody plants (“gulliver” syndrome) (Bond and van Wilgen 1996), and (iii) grazers favour previously burnt areas due to the higher nitrogen values of the re-growing grasses (Mbatha and Ward 2010). As a result of the interspecific competition between grasses and trees (grasses are dominant – Cramer *et al.* 2007), this leads to increased opportunities for recruitment by woody plants.

By evaluating the role of fire in IGR, timely suggestions relating to the manipulation of fire to control woody plant encroachment can be made. Furthermore, other important agents involved in woody plant encroachment, such as grazing herbivores, can be identified and appropriate management strategies formulated. The re-evaluation of fire and the ways in which it may be manipulated to control woody vegetation is important in light of current issues such as climate change.

Methods

Study area

Ithala Game Reserve (IGR) is located in northern KwaZulu-Natal, South Africa (27°30’S, 31°25’E). Prior to the proclamation of IGR, from 1972 to 1982, some of the flatter areas of IGR have been used for crop farming since 1884 (Wiseman *et al.* 2004). Indigenous animals were extirpated by the 1950s as a result of rinderpest and hunting (Wiseman *et al.* 2004). From 1973, a number of animals were

introduced into IGR including the megaherbivores, black rhinoceros (*Diceros bicornis*), white rhinoceros (*Ceratotherium simum*), giraffes (*Giraffa camelopardis*) and elephants (*Loxodonta africana*).

The reserve covers 29 653 ha with the Pongolo River forming the northern boundary of the reserve. The altitude ranges from 320 m a.s.l. at the Pongolo River, to 1 446 m a.s.l. on the southern escarpment plateau. This altitudinal gradient corresponds to high variance in abiotic and biotic components. The landscape types over this altitudinal gradient are complex, ranging from plateaux, scarps, cliffs, deeply incised valleys and floodplains along the Pongolo River (van Rooyen and van Rooyen 2008). Approximately 20% of the reserve has slope gradients that exceed 40°, limiting the distribution of large mammals (le Roux 1985b). The geology of IGR comprises Archaean granite exposures, sandstones, shales, mudstones of the Karoo system and igneous dolerite dykes and sills. The soils of IGR are closely related to the geology, as many are formed *in situ* with underlying rocks. Granites generally form coarse-grained, nutrient-poor soils. Dolerites and diabases produce fertile soils with poorer percolation than soils derived from granites. The predominant soil type in our study area was shallow, rocky lithosols of the Mispah form (van Rooyen and van Rooyen 2008). IGR is a summer rainfall region with a mean annual rainfall of 791 mm. The average daily temperatures in summer are warm to hot (18 – 30°C) and in winter are mild to warm (15 – 25 °C) (Porter 1983).

Vegetation sampling

Vegetation sampling was performed in the vegetation types where fire plays an important role (van Rooyen and van Rooyen 2008). The two broad vegetation types were (i) *Combretum apiculatum* – *Themeda triandra* rocky bushveld (henceforth, *Combretum* woodlands), and (ii) *Trachypogon spicatus* – *Tristachya leucothrix* – *Hyparrhenia hirta* and *Sporobolus africanus* – *Hyparrhenia hirta* old field grasslands (henceforth, old field grasslands) (van Rooyen and van Rooyen 2008). Transects were performed in 2009 to estimate (i) woody plant species richness, (ii) height, (iii) canopy dimensions (longest and shortest orthogonal), (iv) number of stems (10cm above the ground), (iv) stem diameters (10cm above the ground), (v) herbivory damage and (vi) fire damage (herbivory and fire damage were estimated from canopy removal indices in 10% increments). Rockiness was also estimated in two 1m × 1m quadrats at the end of each transect. The mean sward height of the grassy layer was also estimated using a disk pasture meter (Bransby and Tainton 1977) in the old field grasslands. The rocky and undulating nature of the *Combretum* woodlands prevented the use of a pasture disk. In these

woodlands, sward height was estimated within the same 1m × 1m quadrats where rockiness was estimated. The sampling design was randomly-stratified. GPS coordinates of transects were randomly chosen on ArcMap version 9.3 within stratified areas (vegetation type and north-facing slopes). Macrophyllous thickets where fire is excluded were avoided. Therefore, transects were designed so that they did not bisect a buffer of 3m surrounding the shade zone around these thickets. By avoiding the shade zone of thickets, the possibility of sampling the ecotone between the microphyllous and macrophyllous vegetation communities was avoided (Skowno *et al.* 1999). Instead, transects continued linearly away from the 3m buffer zone on the opposite side of the thickets. This enabled a fair comparison of the effects of fire (not effects such as shading) in the *Combretum* woodlands. Each plot consisted of two nested plots for short (0.1 – 1.0m) and tall (>1.0m) woody plants along a 50m transect for taller woody plants. The width and/or length of nested transects for plants >1.0m with <10 individuals was increased to a maximum of 20m × 100m. The minimum size of the nested transects was 10m × 2m for areas with 9 500 indiv. ha⁻¹ in the size class 0.1 – 1.0m. In total, 69 transects were performed.

Historical use of fire in Ithala Game Reserve

The use of fire in IGR has been frequent since the proclamation of the reserve in 1972. Objectives of the use of fire in IGR were described in detail (Porter 1983, le Roux 1985a). The reasons for burning varied between the different vegetation communities of IGR. In woodlands, the ecological factors considered for burning management were to (i) maintain habitat diversity, (ii) maintain the grass component, and (iii) control increasing woody plant densities (le Roux 1985a). To achieve these objectives, biennial burning was performed from late winter to spring where possible (le Roux 1985a). The fire regimes on the old field grasslands were adjusted over time to (i) improve forage quality, (ii) reduce the grass sward height for improved game viewing, and (iii) control woody plant encroachment. These burns were principally performed from early- to mid-winter. Originally, IGR was divided into 18 manageable burning-blocks. Later, these burning blocks were further divided into 22 main blocks. The fuel load provided by the grassy layer was not monitored and estimations of fire intensities were inconsistently recorded by field and technical staff. Field staff were however, prohibited from burning when fuel loads were insufficient, even when burns were scheduled (le Roux 1985a).

Fire data acquisition

Fire scars are mapped by park rangers on 1: 50 000 maps that provide some indication of the extent of burns. The original fire maps were digitized to produce fire frequency maps from 1994 to 2009 using ArcMap version 9.3. The Mean Return Interval (MRI) was calculated as the mean time between each fire event, from 1994 to the last burn.

Data Analysis

Total density

To analyse the effects of fire frequency (FF) on total vegetation density, the FF values for the *Combretum* woodland transects were clustered into 3 FF classes. The FF class value ranges are: low = 0 to ≤ 0.125 , medium = > 0.125 to ≤ 0.25 , high = 0.375 to ≤ 0.5 . In the old field grasslands, the FF value ranges of the low and medium FF classes are similar to those of the *Combretum* woodlands. However, the upper limit of the value range in the high FF class was greater in the old field grasslands (FF = 0.375 to ≤ 1.0), than in the *Combretum* woodlands (0.375 to ≤ 0.5). In the *Combretum* woodlands, the areas burnt annually were unsuitable for comparison with other samples as they generally occurred within ecotones between vegetation types. Therefore, the high FF class in the *Combretum* woodlands had a lower FF value range than in the old field grasslands. To assess the effects of FF on woody vegetation structure, the height range of woody plants in which topkill was most frequent was calculated. The differences in the density of woody individuals, in and above this height range of topkill were assessed between the FF classes. One-way ANOVAs were used to test for significant differences in the density of woody individuals between different FF classes. Significant differences in the density of woody individuals, between the FF classes were assessed using Scheffe *post hoc* tests. The density of individuals in 2.0 – 5.0m height class was square root transformed to satisfy the ANOVA test assumptions in the old field grasslands.

Multivariate analysis

Indirect and direct ordinations were used to assess the relationships between different species densities and FF. For data sets with gradient lengths >2 standard deviations (unimodal), a CA (Correspondence Analysis) was performed instead of a PCA (Principal Components Analysis) that requires gradient lengths <2 standard deviations (linear). Where arching (quadratic distortion) was observed in a CA or

CCA (Canonical Correspondence Analysis), the respective DCA (Detrended Correspondence Analysis) or DCCA (Detrended Canonical Correspondence Analysis) was used to remove the arch effect. For the direct ordinations, the same test for unimodality or linearity of data was applied using detrending analyses (Lepš and Šmilauer 2003).

Species that had inconsistent relationships with environmental gradients between indirect and direct ordinations were omitted from the direct ordinations (their inconsistent relationship with environmental gradients, indicated that the variance in their abundance was not explained by the environmental gradients used (Lepš and Šmilauer 2003)). The significance of the first canonical axis and the combined canonical axes were tested using the Monte Carlo permutation test (Lepš and Šmilauer 2003). For the analysis in the *Combretum* woodlands, transects were clustered into two different groups, a rocky group (40-95% rock cover) and a non-rocky group (0-40% rock cover). The grouping by rockiness removed the 24.32% autocorrelation of rockiness and FF. Slope had a 76.11% and 69.75% covariance with rockiness and altitude, respectively. Thus, the grouping of transects into different rock cover classes enabled us to remove the effects of slope and altitude from the environmental variables in the ordinations (i.e. altitude and slope were redundant due to their high autocorrelation with rockiness). In the old field grasslands grouping by rockiness was unnecessary as all transects were non-rocky and were relatively flat. Topographical data for analyses were obtained from a GIS Digital Terrain Model ($\pm 5\text{m}$ accuracy) using ArcMap version 9.3. Species that represented $\leq 1\%$ of the total abundance of species were excluded from the analyses. In total, 30 species were included in the multivariate analyses in non-rocky areas and 26 species in rocky areas in the *Combretum* woodlands. In the old field grasslands, a total of 26 species were used. CANOCO version 4.5 for Windows was used for multivariate statistical analyses.

Resprouting

Differences in the number of stems per individual woody plant between the three FF classes were tested using one-way ANOVAs. Significant differences among FF classes were identified using Scheffe *post hoc* tests. These tests were performed separately for the *Combretum* woodlands and the old field grasslands.

Topkill, browsing and woody plant mortality

To determine the effects of topkill on woody vegetation, the proportional frequency of topkill was calculated for individuals within six different height classes (0.1 – 0.5m, <1.0m, <2.0m, <3.0m, <5.0m and <8.0m). One-way ANOVAs were used to test for interactions between the low, medium and high FF classes and the proportion of individuals used by browsers, in the *Combretum* woodlands and old field grasslands. A Kruskal-Wallis test was used in the old field grasslands as transformations of the data did not satisfy ANOVA assumptions. Mortality was calculated as the proportion of dead woody plants relative to the total number of live woody plants.

Grass sward height, statistical software and test assumptions

To test the potential role of fire and its associated effects on grass sward height Spearman's rank correlation analyses (untransformed and transformed data did not meet the assumptions for a parametric correlation analysis) were determined for sward height and time since last burn. For all analyses, data were checked so that all assumptions were met for each statistical test. Where assumptions were not met for parametric tests, non-parametric alternatives were used as described. SPSS version 15.0 for Windows was used for univariate statistical tests.

Results

Woody plant species density

Combretum woodlands

The range of density in woody individuals was from 2 500 to 33 600 indiv. ha⁻¹ in this habitat. *Euclea crispa* was the most abundant species in the 0.1 – 1.0m height class and *Dichrostachys cinerea* was the most dominant species in the 1.0 – 8.0m height class (Table 1).

Old field grasslands

The density of woody individuals in the old field grasslands ranged from 90 – 33 400 indiv. ha⁻¹. The dominant species in both the 0.1 – 1.0m and 1.0 – 5.0m height classes was *D. cinerea* (Table 2).

Table 1: Mean density of the 10 most abundant woody species (ranked from 1 = most abundant, to 10 = least abundant) in the 0.1 – 1.0m and 1.0 – 8.0m height classes in rocky bushveld samples.

Height class 0.1 – 1.0m			Height class 1.0 – 8.0m		
Rank	Species	Mean density (indiv. ha ⁻¹ ± S.E.)	Rank	Species	Mean density (indiv. ha ⁻¹ ± S.E.)
1	<i>Euclea crispa</i>	3 064.4 ± 1 108.72	1	<i>Dichrostachys cinerea</i>	798.1 ± 256.70
2	<i>Diospyros lycioides</i>	1 883.8 ± 444.68	2	<i>Combretum apiculatum</i>	254.2 ± 57.02
3	<i>Combretum apiculatum</i>	1 277.8 ± 244.14	3	<i>Acacia caffra</i>	172.2 ± 45.53
4	<i>Acacia karroo</i>	805.4 ± 229.37	4	<i>Gymnosporia buxifolia</i>	151.4 ± 28.69
5	<i>Dichrostachys cinerea</i>	702.1 ± 129.08	5	<i>Acacia karroo</i>	114.8 ± 28.68
6	<i>Hippobromus pauciflorus</i>	451.4 ± 247.57	6	<i>Peltophorum africanum</i>	102.8 ± 46.37
7	<i>Gymnosporia buxifolia</i>	319.9 ± 55.86	7	<i>Dombeya rotundifolia</i>	90.7 ± 47.65
8	<i>Dombeya rotundifolia</i>	285.2 ± 136.52	8	<i>Euclea natalensis</i>	83.3 ± 33.21
9	<i>Acacia caffra</i>	274.8 ± 84.55	9	<i>Terminalia phanerophlebia</i>	65.3 ± 37.36
10	<i>Combretum zeyheri</i>	256.9 ± 61.64	10	<i>Searsia lucida</i>	53.7 ± 34.59

Table 2: Mean density of the 10 most abundant woody species (ranked from 1 = most abundant, to 10 = least abundant) in the 0.1 – 1.0m and 1.0 – 5.0m height classes in old field grasslands.

Height class 0.1 – 1.0m			Height class 1.0 – 5.0m		
Rank	Species	Mean density (indiv. ha ⁻¹ ± S.E.)	Rank	Species	Mean density (indiv. ha ⁻¹ ± S.E.)
1	<i>Dichrostachys cinerea</i>	3 378.8 ± 1054.73	1	<i>Dichrostachys cinerea</i>	1 278.4 ± 1268.5
2	<i>Lippia javanica</i>	2 392.4 ± 733.79	2	<i>Acacia karroo</i>	165.5 ± 174.15
3	<i>Diospyros lycioides</i>	797.0 ± 374.03	3	<i>Lippia javanica</i>	140.5 ± 151.69
4	<i>Acacia karroo</i>	692.4 ± 185.00	4	<i>Searsia lucida</i>	15.8 ± 18.15
5	<i>Ehretia rigida</i>	128.8 ± 106.67	5	<i>Lantana camara</i>	13.3 ± 17.72
6	<i>Grewia caffra</i>	45.5 ± 33.45	6	<i>Gymnosporia buxifolia</i>	12.1 ± 13.78
7	<i>Euclea schimperi</i>	42.4 ± 30.78	7	<i>Pappea capensis</i>	10.3 ± 12.04
8	<i>Sclerocarya birrea</i>	42.4 ± 22.63	8	<i>Combretum apiculatum</i>	6.7 ± 7.72
9	<i>Searsia lucida</i>	37.9 ± 31.01	9	<i>Acacia nilotica</i>	6.1 ± 7.23
10	<i>Scolopia mundii</i>	33.3 ± 18.68	10	<i>Sclerocarya birrea</i>	6.1 ± 7.23

Effects of fire frequency on woody vegetation

Density of woody plants

Combretum woodlands

In the *Combretum* woodlands, the total density of woody individuals did not differ significantly among the FF classes ($F_{2,32} = 0.68$, $p_{0.05} = 0.543$). The height range in which topkill was most frequent was <2m (Figure 7). Therefore, significant differences in the density of woody individuals <2m and >2m in height, were tested. The tests for differences in the density of woody plants <2.0m among the FF classes were non-significant ($F_{2,28} = 1.40$, $p_{0.05} = 0.264$), as was the case for individuals >2.0m ($F_{2,28} = 0.35$, $p_{0.05} = 0.710$).

In the 0.5 – 1.0m height class, the densities of individuals was least in the medium FF class (Figure 1). The density of woody plants in the various height classes approximated a reverse J-shaped distribution (Rao *et al.* 1990). The reverse J-shaped curve signifies constant conditions with continual renewal. The size distribution of populations that exhibited this trend, declined exponentially with increasing size (Rao *et al.* 1990). The relative abundance of individuals in the 0.5 – 1.0m height class in the low and high FF classes indicated a high recruitment rate and/ or a disturbance limiting the growth of individuals (Rao *et al.* 1990, Breebaart *et al.* 2001).

Old field grasslands

The total density of woody individuals differed significantly among the FF groups ($F_{2,27} = 5.448$, $p_{0.05} = 0.010$). Scheffe *post hoc* tests revealed that the high ($p_{0.05} = 0.033$) and low ($p_{0.05} = 0.029$) FF class had a significantly greater total density of woody individuals than the medium FF class. Similar to the *Combretum* woodlands, the height range of woody plants in which topkill was most frequent was <2m (Figure 7). The tests for differences in the density of individuals <2.0m were significant ($F_{2,27} = 3.59$, $p_{0.05} = 0.041$). However, for individuals >2.0m, the differences among FF classes were non-significant ($F_{2,27} = 1.532$, $p_{0.05} = 0.234$). Scheffe *post hoc* tests revealed that the high FF class had a significantly greater density of woody individuals <2.0m ($p_{0.05} = 0.013$) than the medium FF. The overall height class distribution of woody plants in the FF classes in old field grasslands was similar to that of the *Combretum* woodlands (Figure 1).

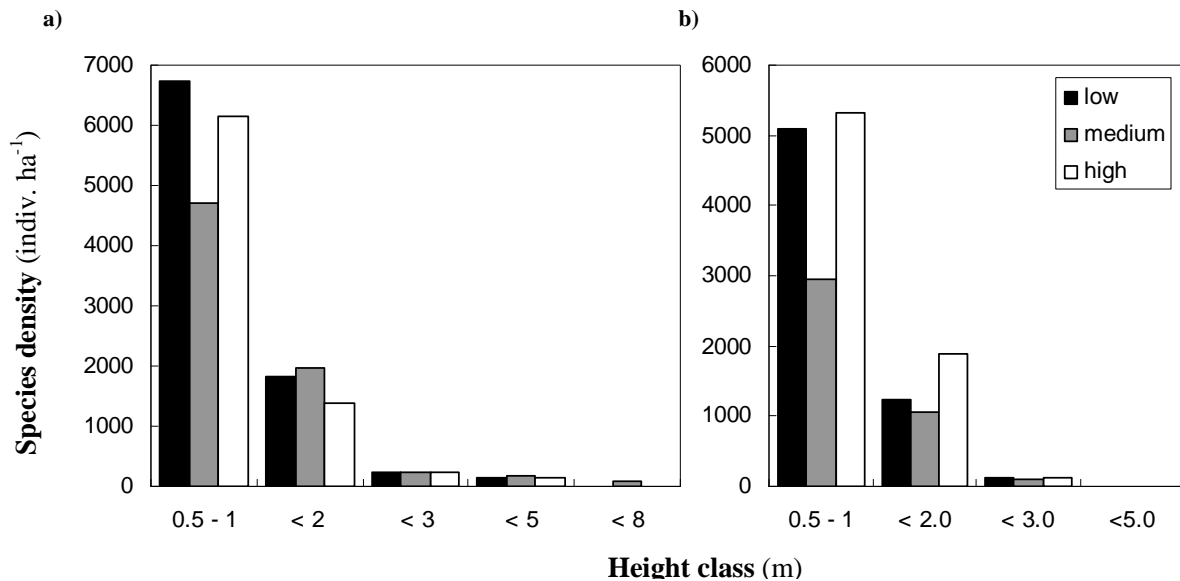


Figure 1: Woody vegetation structural distribution in the (a) *Combretum* woodlands, and the (b) old field grasslands. The value ranges for the FF classes are: low = 0 to ≤ 0.125 m, medium = >0.125 to ≤ 0.25 m, high = 0.375 to ≤ 0.5 m for the *Combretum* woodlands, and for the old field grasslands, high = 0.375 to ≤ 1.0 m.

Multivariate analyses

Combretum woodlands

CCA ordinations were used in the *Combretum* woodlands. The species-environment correlations for axes one and two were: 88.1% and 72.7% for non-rocky areas (Figure 2 (a)) and 88.1% and 88.6% for rocky areas (Figure 2 (b)), respectively. The first canonical axis (non-rocky: $p_{0.05} = 0.046$; rocky: $p_{0.05} = 0.028$) and all canonical axes (non-rocky: $p_{0.05} = 0.046$; rocky: $p_{0.05} = 0.006$) were significant in both non-rocky and rocky areas.

The density of the following species decreased with decreasing FF: *Acacia nilotica*, *Euclea schimperi*, *Lippia javanica*, *Pappea capensis*, *Searsia guenzii*, *Searsia pentheri* and *Searsia lucida*. The density of the following species increased in density with increasing FF: *Diospyros austro-africana*, *Diospyros lycioides*, *Peltophorum africanum*, and *Vitex obovata*. In non-rocky areas, *Euclea crispa* decreased in density with increasing FF and *vice versa* in rocky areas. In rocky areas, *Searsia guenzii* was most dense in areas with intermediate FF.

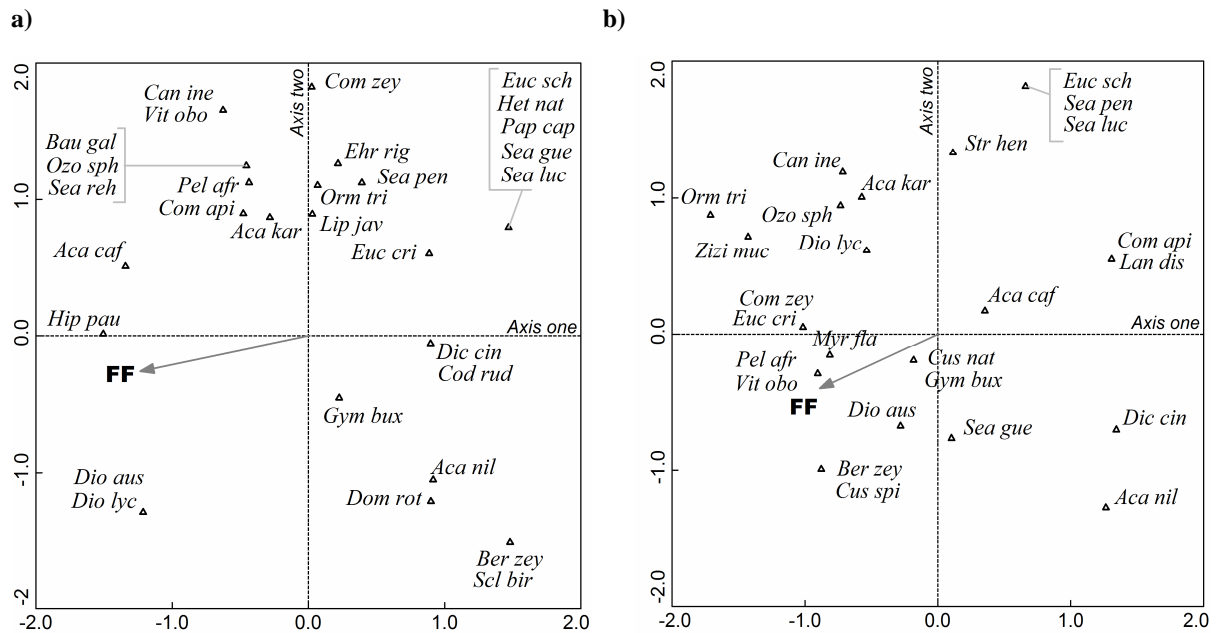


Figure 2: CCA ordinations for (a) non-rocky areas and (b) rocky areas in the *Combretum* woodlands. The ordinations depict the relationship between the density of woody plants and the environmental gradient, fire frequency (FF) (grey arrow). The eigenvalues for axes one and two are 0.284 and 0.146 for (a) and 0.379 and 0.148 for (b), respectively. Triangles outlined in black represent species. Species codes (Appendix 1) that cannot be displayed near their symbol are indicated with light grey lines.

Old field grasslands

A DCCA was used in the old field grasslands. The species-environment correlations for axes one and two were 83.1% and 93.9% respectively (Figure 3). The Monte Carlo permutation tests of the first canonical axis ($p_{0.05} = 0.036$) and all canonical axes ($p_{0.05} = 0.040$) were significant. *Acacia caffra* was identified as an outlier and omitted from the DCCA. The density of *Acacia nilotica* (*Aca nil*), *Ehretia rigida* (*Ehr rig*), *Euclea schimperi* (*Euc sch*), *Grewia caffra* (*Gre caf*), *Pappea capensis* (*Pap cap*), *Searsia lucida* (*Sea luc*), and *Searsia petheri* (*Sea pen*) decreased with increasing FF. The density of *Dombeya rotundifolia* increased with increasing FF.

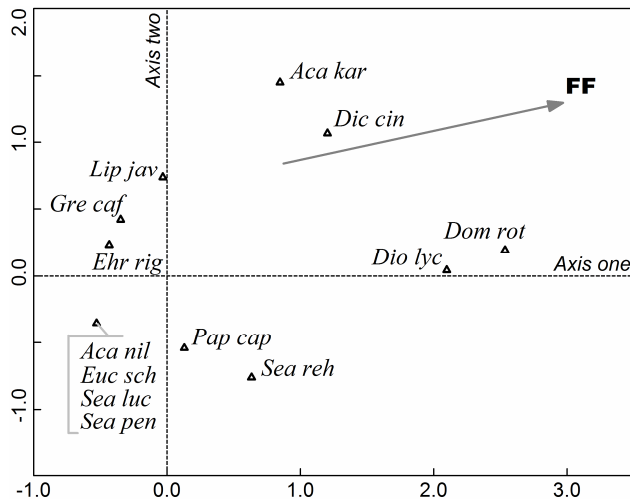


Figure 3: DCCA depicting the relationship between woody species densities in the old field grasslands and the environmental variable FF (grey arrow). Note that the environmental gradient, FF, does not begin at the origin (0, 0) on the canonical axes due to the rescaling of axes in a detrended analysis (Lepš and Šmilauer 2003). The eigenvalues for axes one and two are 0.169 and 0.028, respectively. Triangles outlined in black represent species. Species codes (Appendix 1) that cannot be displayed near their symbol are indicated with light grey lines.

Population size structure and fire frequency

Combretum woodlands

The density of individuals >8.0m was low compared to the density of shorter individuals of all species (Figure 4). A number of the dominant species had a reverse J-shaped population structure distribution (Rao *et al.* 1990). *Acacia karroo*, *Combretum apiculatum* and *Dichrostachys cinerea* displayed the general reverse-J shaped distribution in the *Combretum* woodlands. The density of *C. apiculatum* and *A. karroo* individuals <2m were greatest in medium FF class. *C. apiculatum* and *A. karroo* individuals >2m were most abundant in the high FF class. The abundance of *D. cinerea* generally decreased with increasing FF.

Euclea crispa and *Diospyros lycioides* displayed an L-shaped population structure. An L-shaped population structure is typified by an abundance of individuals in the smallest height class and

few or no individuals in the larger height classes (Masaki *et al.* 1992, Breebaart *et al.* 2001). The L-shape distribution may be due to a number of factors such as exceptional recruitment, mortality of individuals >1m or individuals caught within the “fire trap” (Masaki *et al.* 1992, Bond and Midgley 2000, Breebaart *et al.* 2001).

Searsia lucida individuals were most abundant in the 1–2m height class in low FF areas. In the intermediate FF areas, *S. lucida* individuals were lacking or absent. The density distribution of *Acacia caffra* was variable across the height classes. This may signify either limited sampling of this species or definite pulses of recruitment within the various FF classes (Rao *et al.* 1990, Breebaart *et al.* 2001). Individuals >1.0m of *A. caffra* in the intermediate FF classes displayed a reverse-J shaped curve. In the high FF class, the density of *Gymnosporia buxifolia* individuals decreased sharply in the height categories >1.0m. In the low and medium FF class, *G. buxifolia* displayed a weak reverse J-shaped curve. The weak reverse J-shaped curve indicates that some disturbance has limited recruitment and/or growth of a species (Rao *et al.* 1990, Breebaart *et al.* 2001).

Old field grasslands

Densities of individuals >2.0m were low (Figure 5). *D. cinerea* displayed a reverse-J shaped distribution and its density was lowest in areas with intermediate FFs. The density distribution of *A. karroo* individuals was L-shaped in the medium and high FF classes (Masaki *et al.* 1992, Breebaart *et al.* 2001). The highest density of *A. karroo* was in areas with high FFs and lowest in areas with low FFs. *Lippia javanica* also displayed an L-shaped distribution (Masaki *et al.* 1992, Breebaart *et al.* 2001).

Resprouting

The number of stems per woody plant significantly differed among FF classes in the old field grasslands ($F_{2, 28} = 41.77$, $p_{0.05} < 0.001$) (Figure 6). Scheffe *post hoc* tests revealed that the significant differences were between each of the FF classes (the low and medium FF class, $p_{0.05} < 0.001$; the medium and high FF classes, $p_{0.05} < 0.001$ and the low and high FF class, $p_{0.05} < 0.001$). In the *Combretum* woodlands, there were no significant differences in the number of stems per individual among the FF classes ($F_{2, 32} = 0.534$, $p_{0.05} = 0.591$).

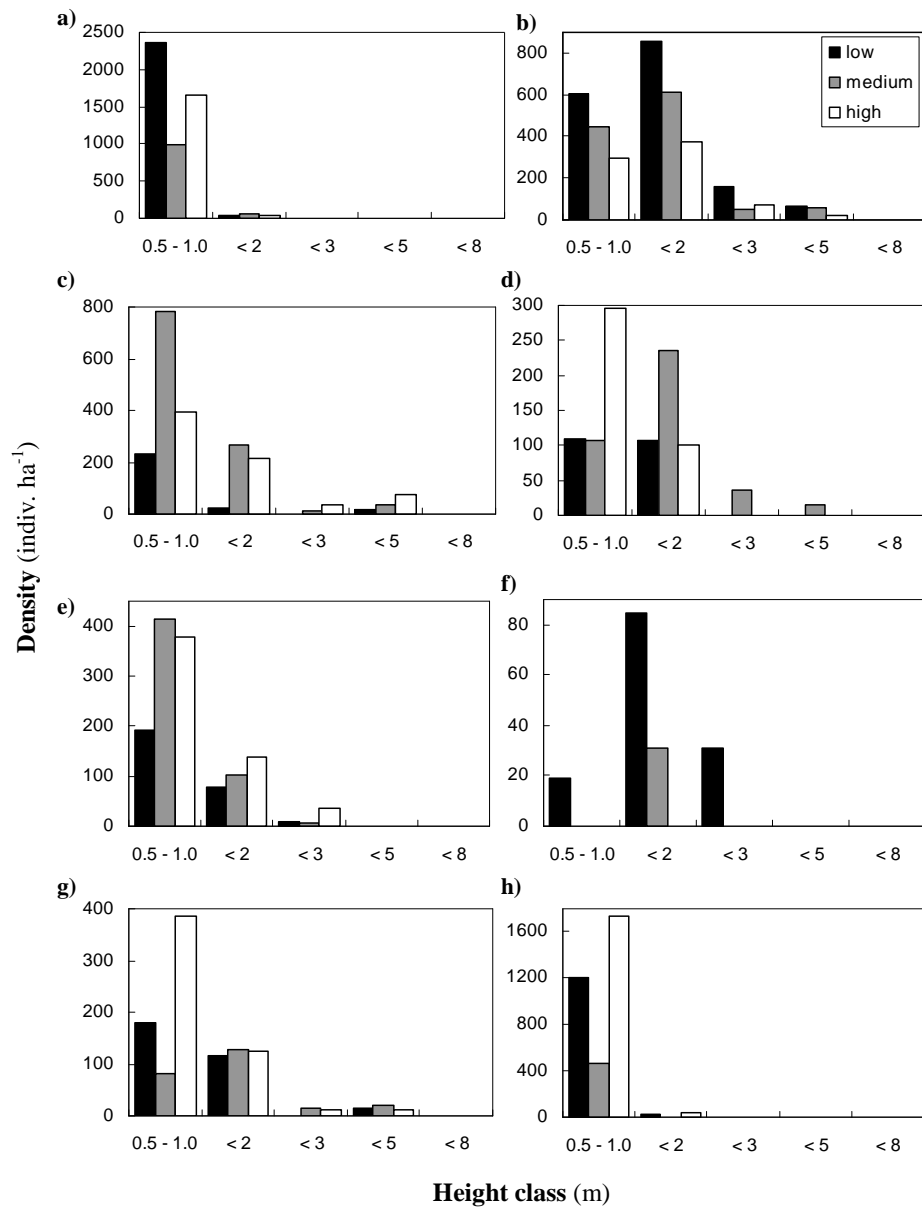


Figure 4: Density of woody species in different height classes within the different FF classes in the *Combretum* woodlands. The FF classes are indicated in the legend in the top right hand corner of the figure. The values for the FF classes are; low = 0 to ≤ 0.125 , medium = > 0.125 to ≤ 0.25 , high = 0.375 to ≤ 0.5 . The woody species are: (a) *Euclea crista*, (b) *Dichrostachys cinerea*, (c) *Combretum apiculatum*, (d) *Acacia caffra*, (e) *Acacia karroo*, (f) *Searsia lucida*, (g) *Gymnosporia buxifolia* and (h) *Diospyros lycioides*.

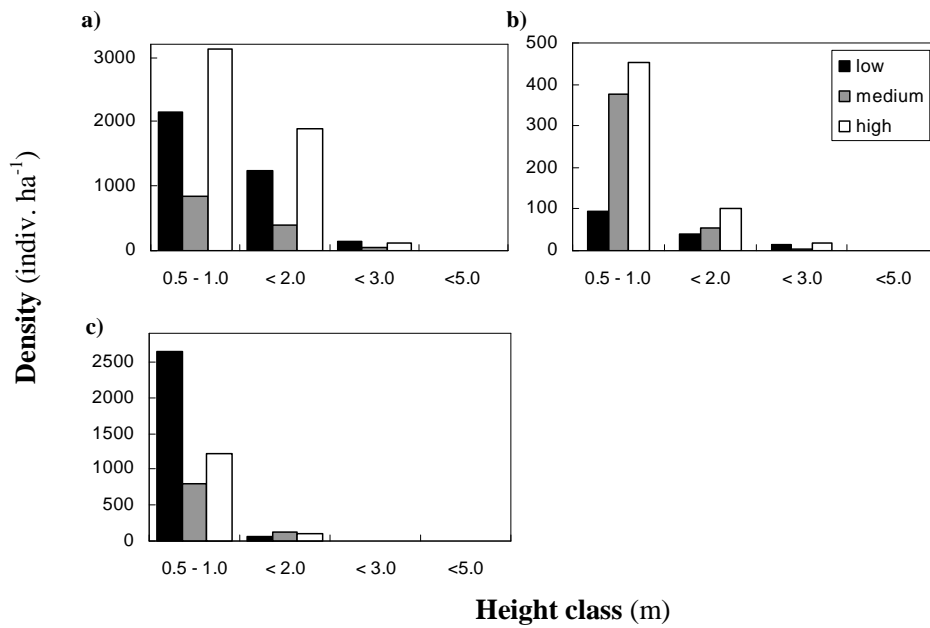


Figure 5: Density of woody species in different height classes within the different FF classes (see legend) in the old field grasslands. The value ranges for the FF classes are; low = 0 to ≤ 0.125 , medium = > 0.125 to ≤ 0.25 , high = 0.375 to ≤ 1.0 . The woody species are: (a) *Dichrostachys cinerea*, (b) *Acacia karroo* and (c) *Lippia javanica*.

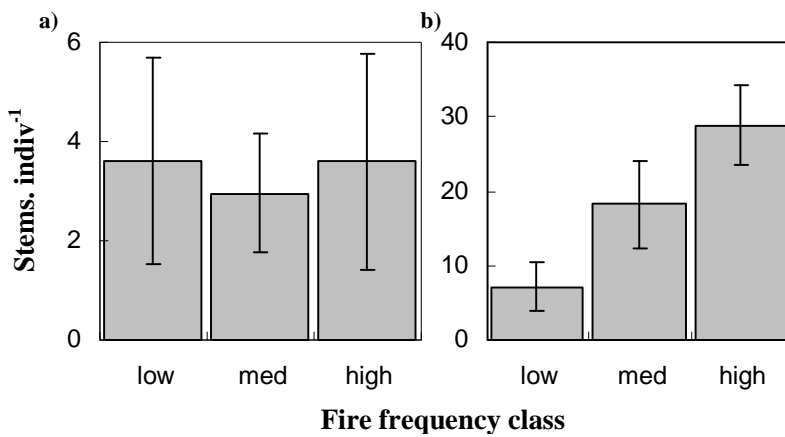


Figure 6: Distribution of the number of stems per individual in the (a) *Combretum* woodlands and (b) old field grasslands, in their respective FF classes. The error bars represent \pm S.D.

Topkill, browsing and woody plant mortality

The proportional frequency of topkill decreased rapidly from the 1.0 – 2.0m to the 2.0 – 3.0m height class (Figure 10). Woody plants 0.1 – 2.0m received similar amounts of topkill. The number of dead woody individuals was low. The highest mortality in a single transect was five *Dichrostachys cinerea* individuals <1.0m (of 108 individuals in total). These individuals were located in an area that was burnt annually in the old field grasslands. The overall mortality was 0.43% in the old field grasslands and *Combretum* woodlands. Besides *D. cinerea*, the only other species observed to suffer mortality were one or two individuals of *Searsia lucida*, *Dombeya rotundifolia*, and *Combretum apiculatum*.

There were no significant interactions between the proportion of browsed species and the low, medium and high FF classes (*Combretum* woodlands: $F_{2,30} = 0.89$, $p_{0.05} = 0.418$; old field grasslands, Kruskal-Wallis test, $H_2 = 1.82$, $p_{0.05} = 0.403$). There was no mortality of woody plants due to browsing alone. Two *D. cinerea* individuals >3.5m had suffered mortality from the combined ~70% canopy removal by elephants and scorching by fire. The most notable effect of browsing observed was caused by giraffe (*Giraffa camelopardis*) (Bond and Loffell, 2001). A transect in the old field grasslands, contained a stand of *A. karroo* that had been maintained at a height of ~2.5m by giraffes. This transect was therefore omitted from analyses because of the confounding effects of browsing on measuring the effects of FF on woody vegetation.

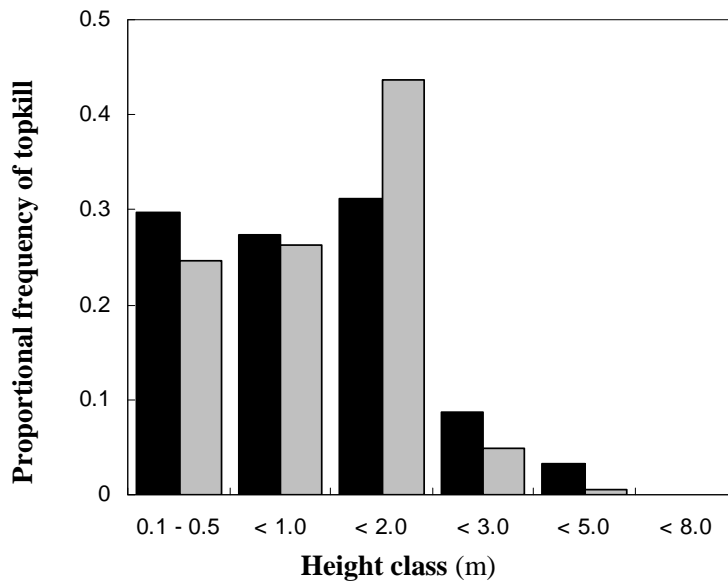


Figure 7: Proportional topkill or above-ground stem death of woody plants by fire per height class in the *Combretum* woodlands (black bars) and old field grasslands (grey bars).

Grass sward height

No significant correlation was found between the time since the last burn and grass sward height in the *Combretum* woodlands ($(r_s)_{0.05(2), 33} = -0.100, p_{0.05} = 0.562$) and in the old field grasslands ($(r_s)_{0.05(2), 33} = 0.235, p_{0.05} = 0.167$). Notably however, 17 samples (total $n = 69$) within the range of 10 – 40 months since the last burn had a ~7 fold greater sward height than other samples burnt at similar periods. Some swards ($n = 9$) remained relatively short (<10cm) despite the relatively long time since the last burn (<36 months).

Discussion

Although the effects of FF on woody vegetation have reportedly been variable (Hoffmann 1999, Higgins *et al.* 2007), this study has highlighted a number of important effects of FF on woody vegetation. The prediction that the total density of woody plants would decrease with increasing FF was not supported. In the old field grasslands we found that areas burnt most frequently had a

significantly higher density of woody individuals. In the *Combretum* woodlands however, there were no significant trends in the total density of woody plants and FF classes. In the *Combretum* woodlands, the increased variability in dominant species trends (figure 4) added to the variation in the trends of total woody plant density with FF classes. Furthermore, the increased upper range of FF values in the old field grasslands, compared to the *Combretum* woodlands, is hypothesized to have added to the differences in trends of total density of woody individuals among the FF classes.

The expected dominance of shorter woody plants in areas with high FFs was not evident in the *Combretum* woodlands. In areas burnt annually (old field grasslands) the density of shorter (<2.0m) woody individuals was significantly greater than in areas burnt at medium FFs. The dominance of smaller individuals in areas with high FFs, as observed in the old field grasslands, has been interpreted as evidence for the “gulliver” syndrome (Higgins *et al.* 2000, Higgins *et al.* 2007). Frequent fires have been able to prevent the recruitment of “gullivers,” keeping them relatively short (Higgins *et al.* 2000, Higgins *et al.* 2007). An understanding of the biology of the dominant species’ reactions to fire is useful in the interpretation of the observed trends in total density changes among the different FF classes. *Dichrostachys cinerea* and *Acacia karroo* have been documented as problematic encroachers and have increased in density despite the use of fire (Wakeling and Bond 2007, Balfour and Midgley 2008, Munkert 2009). Fire-herbivore interactions during woody plant establishment also facilitate the understanding of some of the observed trends of species density with FF (Archibald *et al.* 2005, Danell *et al.* 2006).

In the old field grasslands, the density of *D. cinerea* was higher in areas burnt most often (FF = 0.375 to ≤ 1.0 burns. yr⁻¹) and burnt the least (0.125 to ≤ 0.25 burns. yr⁻¹), compared to areas burnt at medium FFs. Wakeling and Bond (2007) found that in Hluhluwe-iMfolozi Nature Reserve, that *D. cinerea* reproduced 45% sexually and 55% asexually by root suckering. They also found that the disturbance type (grazing and fire frequency) had no significant effect on the reproduction mode. Nevertheless, the ability to root sucker makes *D. cinerea* and *A. karroo* problematic encroachers (Wakeling and Bond 2007, Munkert 2009). The significant increase in resprouting with increasing FF confirms the vigorous resprouting ability of species such as *D. cinerea* and *A. karroo* in the old field grasslands (Figure 6) (Roques *et al.* 2001, Moleele *et al.* 2002, Tobler *et al.* 2003, Wakeling and Bond 2007, Munkert 2009). This vigorous resprouting ability explains the ability of these encroaching microphyllous species to survive in areas burnt annually.

There was an important difference in the trends in density of *D. cinerea* and *A. karroo* with FF. In both the *Combretum* woodlands and the old field grasslands, *A. karroo* increased in density with increasing FF. This may occur because *A. karroo* is considered to be a vigorous resprouter (Balfour and Midgley 2008) and is able to survive the frequent cool fires in IGR (Ruinard, pers. comm.). Therefore, under the current fire regime, *A. karroo* may be more difficult to control than *D. cinerea*, especially in the *Combretum* woodlands where *D. cinerea* population density was negatively related to fire frequency.

The high density of woody individuals in areas with low FFs may be attributable to the: (i) release from fire (Balfour and Midgley 2008), and (ii) the general positive impact of grazing on woody plant establishment (Danell *et al.* 2006). Areas that were burnt the least were either protected from fire or incapable of burning due to insufficient fuel loads. Grazing herbivores are known to be attracted by the green flush of recently burnt areas (Fuhlendorf and Engle 2004, Archibald *et al.* 2005). The local concentrations of grazing herbivores have retarded the accumulation of fuel for burning in some areas of the old croplands. The reduction of grassy fuel for fires prevented IGR management from burning some areas, resulting in the recorded lower FFs (Wiseman *et al.* 2004). The lower FFs have allowed the establishment of some woody plants such as *D. cinerea* (Higgins *et al.* 2000, Balfour and Midgley 2008). Higher levels of grazing have been shown to be positively related to woody plant establishment through processes such as seed deposition and a reduction in grass vigour (Jeltsch *et al.* 2000, Danell *et al.* 2006, Riginos 2009). Therefore, a suppression of fire and the concentration of grazing herbivores may explain the higher density of *D. cinerea* densities in low FF areas.

The minimal effect of browsing on woody plant mortality indicates that browsers had little effect on woody plant density. Browsing may however have added to some of the variation observed in woody vegetation structure (Hester *et al.* 2006). Furthermore, in this study, the non-significant relationship between FF and the proportion of species browsed by herbivores demonstrates that browsing was not related to FF. Other factors involving positive feedbacks with browse may have influenced the spatial concentration of browsers (du Toit *et al.* 1990). Browsers may stimulate a compensatory response in *Acacia* species. Above certain thresholds of browsing, trees may concentrate nutrients for regrowth to browsed shoots. The supply of nutrients to browsed shoots is maintained by constant browsing, simulating a “browsing lawn” (du Toit *et al.* 1990). This was evident in areas of the old field grasslands where giraffes concentrated their browsing efforts, reducing the height of *A. karroo*

trees. These areas were avoided for sampling because of the influence of the giraffe on reducing woody vegetation height.

Another factor that may have allowed the establishment of woody plants in areas with higher FFs, is that the intensity of fires has been inadequate in causing a high proportion of topkill (Trollope and Tainton 1986). *D. cinerea* individuals up to ~3m may suffer stem death in intense fires (pers. obs.). Woody plants have typically been considered to have escaped the effects of intense fires at the height of $\geq 4\text{m}$ (Trollope and Tainton 1986). In IGR however, topkill mostly affected trees $< 2.0\text{m}$ high (Figure 7). This low height of topkill would have allowed woody plants to escape the effects of fire at half of the normal height (Trollope and Tainton 1986). Meyer *et al.* (2005) found that larger trees may be more susceptible to mortality from topkill than smaller trees. In IGR however, 71.4% of the woody plants that suffered mortality from fire in IGR were $< 1.0\text{m}$. This suggests that in IGR, shorter (e.g. *D. cinerea*) woody individuals have been more susceptible to fire-induced mortality. The overall mortality rate of woody plants in all height classes was low (0.43%), demonstrating that fire had minimal direct effects on woody plant density (see also Meyer *et al.* 2005).

In the *Combretum* woodlands, the reason for the decrease of *D. cinerea* with increasing FF may be due to a number of factors. The higher upper limit of the FF class value range in the old field grasslands (0.375 to ≤ 1.0), compared to that of the *Combretum* woodlands (FF=0.375 to ≤ 0.5) could have influenced the difference in *D. cinerea* density. The overall vigour of the grassy layer in the old field grasslands would be expected to be reduced in the *Combretum* woodlands. This is because of the alteration of the burning regime to reduce grass vigour and height of the tall *Hyparrhenia hirta* grass stands (le Roux 1985a). It appears therefore that annual burns are conducive to increases in *D. cinerea* density in the old field grasslands, and biennial burns are conducive to decreases in *D. cinerea* density, in the *Combretum* woodlands.

The high density of woody plants in the *Combretum* woodlands and old field grasslands were affected by the high densities of *Euclea crispa* and *Diospyros lycioides*. Excavation of the roots of *E. crispa* plants suggested that one individual may resprout a number of times $> 3\text{m}$ away from an individual (pers. obs.). Similarly, the excavation of *D. lycioides* revealed thick roots and resprouting ability allowing the formation of large dense clumps (pers. obs.). Therefore, the high density of *E. crispa* and *D. lycioides* individuals was misleading when interpreting total species densities. The > 3.5 fold lower abundance of *E. crispa* on deeper soils (with low rock cover) suggests that it establishes

preferentially on shallow soils (with high rock cover). This also explained the comparatively low density of *E. crispera* on the old field grasslands that have deeper, non-rocky soils.

The density of both *D. lycioides* and *E. crispera* was lowest in areas with medium FFs (except in the larger 1.0 – 2.0m height class where *E. crispera* is only slightly more abundant (~25 indiv. ha⁻¹)) (Figure 4). In the high FF areas, this result suggests that disturbances such as fire and the concentration of grazing herbivores give these species the opportunity to encroach. Disturbance in the low FF class may also explain the encroachment of these two species as described for *D. cinerea*. As in the old field grasslands, large areas of the *Combretum* woodlands had experienced a low FF due to insufficient fuel load accumulation. The insufficient fuel load accumulation signifies a decrease in grass vigour resulting from a concentration of grazing herbivores and/ or drought (Crider 1955, van Langevelde *et al.* 2003, Riginos 2009). The decrease in grass vigour in areas with low FFs are hypothesized to result in the increase of *E. crispera* and *D. lycioides*. The reported herbivory of *E. crispera* in IGR has been low (Wiseman *et al.* 2004). The release of *Euclea* species (e.g. *E. crispera*) from herbivory (because of their unpalatability, due to the presence of naphthoquinones and triterpenoids (Watt and Breyer-Brandwijk 1962, Hutchings *et al.* 1996, Bertolli 2009)) has given them a competitive advantage over grasses and added to their ability to encroach on grasslands in IGR.

Vegetation composition was significantly affected by FF. Evergreen macrophyllous species such as eucleas (*E. natalensis* and *E. schimperi*), and *Searsia lucida* generally decreased in density with increasing FF. Interestingly, one of the microphyllous species *A. nilotica* decreased in density with increasing FF. However, *A. nilotica* is known to be more pyrophobic than other acacias such as *A. karroo*, explaining its aversion to frequent fires (Figure 2 and 3) (Midgley and Bond 2001). *Euclea* species have been described as vigorous resprouters (Skowno *et al.* 1999). However, medium to high FFs are a useful tool for controlling the establishment of these species (Figure 2 and 3) (Skowno *et al.* 1999). *E. schimperi* and *E. natalensis* are macrophyllous species, and have been known to increase in density with the suppression of fire and replace microphyllous species (Skowno *et al.* 1999).

In areas burnt annually, the higher density of encroaching microphyllous species was prompted by fire. In these areas, should the vigour of the grassy layer decrease, the frequency of intense fires would decrease (Trollope and Tainton 1986, Balfour and Midgley 2008). The suppression of fire may allow the encroaching species to grow taller and would become dominant as a consequence (Higgins *et al.* 2000, Higgins *et al.* 2007). Then, a number of outcomes may follow:

(1) The general structure of the encroached thicket may be maintained by herbivores such as elephants (Kalwij *et al.* 2010, Midgley *et al.* 2010). Such herbivory has also been known to change species composition to a less palatable state (Holdo 2007, Midgley *et al.* 2010).

(2) The self-thinning of the patch and reversion to a non-encroached state should occur (White and Harper 1970, Wiegand *et al.* 2006). The combined action of fire, herbivory by elephants, and climate (e.g. frost) has also been shown to facilitate the reversion of closed woodlands to open savanna (Dublin 1991, Holdo 2007, Midgley *et al.* 2010).

(3) The development of a closed macrophyllous woody plant community may occur (Skowno *et al.* 1999). The development of closed *Euclea* thickets following the suppression of fire has been described to occur within a decade (Skowno *et al.* 1999). In addition, macrophyllous species have been observed to suppress the herbaceous layer and result in decreased fire intensities and frequencies (Skowno *et al.* 1999, Hoffmann *et al.* 2003, Gignoux *et al.* 2009). The suppression of the herbaceous layer would further extend the longevity of these macrophyllous thickets (Skowno *et al.* 1999, Gignoux *et al.* 2009). Rare events, such as extremely hot fires (Ikeckukwu Muoghalu 2006) may however convert these macrophyllous thickets to a more open state (Hoffmann *et al.* 2003). In all of the above three scenarios, fire is an important agent in the prevention of bush encroachment and the development of macrophyllous thickets that are resistant to fire.

Conclusions

Fire has played an important role in woody vegetation in IGR. The effects of the fire regime on the total density of woody plants differed in the *Combretum* woodlands and old field grasslands. In the old field grasslands, annual burns resulted in a significant increase in short microphyllous encroachers, such as *D. cinerea* and *A. karroo*. In the *Combretum* woodlands, the effect of FF on the total density of woody plants was non-significant due to the increased variability in dominant species trends with FF, and the decreased upper range of FF values compared to the old field grasslands. However, in both vegetation types, the density of woody plants was lowest in areas with intermediate FFs. The release of woody vegetation from fire and/ or the concentration of grazing herbivores in areas with low FFs resulted in an increase in woody vegetation density. For effective control of the encroaching trees, an

intermediate fire frequency (one burn every 2 to 4 years) is required. Furthermore, the intensity of the fires must be sufficient to increase topkill (Balfour and Midgley 2008).

Grazing herbivores have also played an important role in facilitating the encroachment of a number of woody species (Archer 1995, Roques *et al.* 2001, Danell *et al.* 2006). Where possible, burns must be strategically timed and placed to spread the impacts of herbivores on the grassy layer to allow sufficient accumulation of grassy biomass to fuel fires (Archibald *et al.* 2005). This study has also highlighted the importance of fire in suppressing the development of macrophyllous thickets. Therefore, management should aim to foster the development of grassy biomass for fuel for fires. This strategy may prevent the rapid conversion of microphyllous woody savannas into macrophyllous woody communities that are resistant to fire (Skowno *et al.* 1999, Bond and Archibald 2003).

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Appendix 1:

Table 3: Species code names

Species code	Species name	Species code	Species name
Aca caf	<i>Acacia caffra</i>	Het nat	<i>Heteropyxis natalensis</i>
Aca kar	<i>Acacia karroo</i>	Hip pau	<i>Hippobromus pauciflorus</i>
Aca nil	<i>Acacia nilotica</i>	Lan cam	<i>Lantana camara</i>
Bau gal	<i>Bauhinia galpinii</i>	Lan dis	<i>Lannea discolor</i>
Ber zey	<i>Berchemia zeyheri</i>	Lip jav	<i>Lippia javanica</i>
Can ine	<i>Canthium inerme</i>	Myr fla	<i>Myrothamnus flabellifolius</i>
Com api	<i>Combretum apiculatum</i>	Orm tri	<i>Ormocarpum trichocarpum</i>
Com zey	<i>Combretum zeyheri</i>	Ozo sph	<i>Ozoroa spherocarpa</i>
Cus spi	<i>Cussonia spicata</i>	Pap cap	<i>Pappea capensis</i>
Dic cin	<i>Dichrostachys cinerea</i>	Pel afr	<i>Peltophorum africanum</i>
Dio aus	<i>Diospyros austro-africana</i>	Scl bir	<i>Sclerocarya birrea</i>
Dio lyc	<i>Diospyros lycioides</i>	Sco mun	<i>Scolopia mundii</i>
Dom rot	<i>Dombeya rotundifolia</i>	Sea gue	<i>Searsia gueinzii</i>
Ehr rig	<i>Ehretia rigida</i>	Sea luc	<i>Searsia lucida</i>
Ekb cap	<i>Ekebergia capensis</i>	Sea pen	<i>Searsia pentheri</i>
Euc cri	<i>Euclea crispa</i>	Sea reh	<i>Searsia rehmanniana</i>
Euc nat	<i>Euclea natalensis</i>	Str hen	<i>Strychnos henningsii</i>
Euc shr	<i>Euclea schimperi</i>	Ter pha	<i>Terminalia phanerophlebia</i>
Gre caf	<i>Grewia caffra</i>	Vit obo	<i>Vitex obovata</i>
Gym bux	<i>Gymnosporia buxifolia</i>	Xim caf	<i>Ximenia caffra</i>
Gym sen	<i>Gymnosporia senegalensis</i>	Ziz muc	<i>Ziziphus mucronata</i>

Chapter 4:

Conclusions

The role of fire in controlling bush encroachment in savannas has been highlighted in the literature (Higgins *et al.* 2000, Bond and Keeley 2005). Recently, with the global occurrence of bush encroachment (Ward 2005, Balfour and Midgley 2008, Ward 2010), fire has come under increasing scrutiny (Bond and Archibald 2003, van Wilgen *et al.* 2004, Govender *et al.* 2006, van Wilgen 2009, Archibald *et al.* 2010). The role of fire has been distinctive in preventing the formation and expansion of evergreen macrophyllous thickets (containing for example *Euclea* and *Searsia* spp.) in savannas (Skowno *et al.* 1999, Hoffmann *et al.* 2003, Gignoux *et al.* 2009). However, the role of fire in controlling the structure and density of vigorous deciduous microphyllous resprouters (e.g. *Acacia karroo* and *Dichrostachys cinerea*) has been questioned (Wakeling and Bond 2007, Balfour and Midgley 2008).

Isolated deciduous microphyllous woody plants are typically more resistant to fire than evergreen macrophyllous woody individuals (Hoffmann *et al.* 2003). Microphyllous woody plants have a comparatively thicker layer of bark that insulates them against damage by fire (Hoffmann *et al.* 2003). The clustering of evergreen macrophyllous woody plants to form thickets does however protect them against fire (Hoffmann *et al.* 2003). Evergreen macrophyllous thickets suppress the herbaceous layer and have a humid dense canopy, reducing the flammability of these thickets. Furthermore the leaves of evergreen macrophyllous woody plants are less flammable than deciduous microphyllous plants (Skowno *et al.* 1999, Hoffmann *et al.* 2003, Gignoux *et al.* 2009). These factors suppress the effectiveness of fire moving through evergreen macrophyllous thickets, adding to their resistance to fire (Skowno *et al.* 1999, Hoffmann *et al.* 2003, Gignoux *et al.* 2009).

Although fire has been successful in controlling the expansion and formation of evergreen macrophyllous thickets, some of the effects of fire on deciduous microphyllous woody vegetation have been unpredictable (Higgins *et al.* 2007, Wakeling and Bond 2007, Balfour and Midgley 2008). The effect of fire has been demonstrated on microphyllous woody vegetation by reducing plant height (Higgins *et al.* 2000, Higgins *et al.* 2007). However, in some areas, increased fire frequency has resulted in a decrease in the density of microphyllous woody plants (Hoffmann 1999); in others

however, no significant effect has been observed (Higgins *et al.* 2007). Furthermore, global warming and climate change has added further uncertainty regarding the dynamics of tree:grass dynamics in savannas (Bond and Midgley 2000, Kgope *et al.* 2010). In IGR, fire was found to play an important role in both microphyllous and macrophyllous woody vegetation dynamics.

The remote sensing technique, textural analysis, used in this study showed that mean woody vegetation cover (+32.5%) and density (+657.9 indiv. ha⁻¹) increased significantly from 1943 to 2007. The increase in woody vegetation from 1943 to 1969 (before the proclamation of IGR in 1972) corresponds to the general increase in grazing by livestock in the area since 1884 (Porter 1983, Wiseman *et al.* 2004). This observation corresponds to the predictions of Walter's two-layer model (1939) of tree:grass coexistence by root niche separation (Walter 1939). The application of the two-layer model predicts that under heavy grazing, grass vigour decreases and water percolation into deeper soil layers increases (Walter 1939). Woody plants that have roots penetrating deeper into the soils would then have increased water availability and outcompete grasses (Walter 1939). The assumption of root niche separation between woody and grassy plants is however incorrect (Ward 2005). For example, some savanna soils are too shallow to allow the woody:grassy root niche separation by soil depth (Wiegand *et al.* 2005).

Despite the functional problems of Walter's (1939) two-layer model, the prediction that grazing may facilitate bush encroachment has been supported by more recent findings (Bond 2008, Riginos 2009, Ward and Esler 2010). Grasses have been demonstrated to be important competitors against woody plants (Bond 2008, Riginos 2009, Ward and Esler 2010). Compared to woody plants, grasses are rapid responders to pulsed resources (Chesson *et al.* 2004) and may limit the availability of resources to woody plants, within similar and different soil layers (Knoop and Walker 1985, Riginos 2009, Cramer *et al.* 2010). Therefore, a reduction in grass vigour may enhance the competitive ability of woody plants in savannas (Cramer *et al.* 2010). This reduction of grass vigour, caused by heavy grazing, may therefore facilitate bush encroachment (Bond 2008).

Another effect of increased grazing from 1972 to 2007 in IGR was a reduction in grassy biomass or fuel for fire. Consequently, the fire frequency declined from a biennial rate to zero burns per year from 1972 to 2007. The complete suppression of fire, from 1990 to 2007, led to a rapid invasion of woody plants in some areas of IGR. This demonstrates the importance of fire in controlling woody vegetation encroachment in IGR. The study by Skowno *et al.* (1999) also highlighted the fact

that the suppression of fire may lead to the rapid encroachment of woody plants into savannas, within a decadal time scale.

The field component of this study, in Chapter 3, also highlighted the importance of fire in woody vegetation dynamics. In general, the highest density of encroaching woody species was at intermediate frequencies (0.25 – 0.5 burns per annum). The encroaching species (*Dichrostachys cinerea*, *Acacia karroo*, *Euclea crispa* and *Diospyros lycioides*) were found to have vigorous resprouting capabilities. There was an important difference in the trends in density of *D. cinerea* and *A. karroo* with fire frequency. In both the *Combretum* woodlands and the old field grasslands, *A. karroo* increased in density with increasing fire frequency. This may occur because *A. karroo* is a vigorous resprouter (Balfour and Midgley 2008) and is able to survive the frequent cool fires in IGR. Therefore, under the current fire regime, *A. karroo* may be more difficult to control than *D. cinerea*, especially in the *Combretum* woodlands where *D. cinerea* population density was negatively related to fire frequency.

To explain the trends in the density of the encroaching woody plants with fire frequency, it is important to consider the interactions between fire and herbivory (Archibald *et al.* 2005). In areas that have low fire frequencies, the higher density of woody plants was attributed to the (i) release from fire (Balfour and Midgley 2008), and (ii) the general positive impact of grazing on woody plant establishment (Danell *et al.* 2006). Particularly, the suppression of hot fires that cause higher proportions of topkill (as found in Hluhluwe-iMfolosi game reserve by Balfour and Midgley 2008) has probably facilitated the release of woody encroachers in IGR.

The general positive influence of herbivores on woody plant germination may have also facilitated encroachment (Danell *et al.* 2006). The concentration of herbivores (shown by the maintenance of a short (<10cm) grass sward) due to increased nitrogen on these swards (see e.g. Mbatha and Ward 2010), may result in the formation of ‘grazing lawns’ (*sensu* McNaughton 1984). Due to the positive feedback that results from the increased grazing, high N levels are maintained (McNaughton 1984). Interestingly, in the old field grasslands, areas that had higher fire frequencies (~annual) had higher densities of short (<2m) encroaching microphyllous woody plants. *Dichrostachys cinerea* and *Acacia karroo* were the principal encroaching species in the old field grasslands. Both of these species have been demonstrated to be vigorous resprouters, reproducing asexually (including by root suckering) in areas with frequent fires (Walters *et al.* 2004, Wakeling and Bond 2007, Balfour and Midgley 2008, Munkert 2009, Wigley *et al.* 2009). In addition, herbivores have been shown to be

attracted to recently burnt areas (Archibald *et al.* 2005). Therefore the areas burnt annually may be expected to be frequented by grazers (Archibald *et al.* 2005). The high density of these encroaching trees in areas burnt annually may be explained by their vigorous resprouting behaviour and the frequent attraction of herbivores to areas burnt annually which reduces grass competition and creates open spaces for tree germination (Archibald *et al.* 2005).

The predictions of Higgins *et al.* (2000) were also supported by this study. In areas burnt frequently and infrequently, the mortality of woody individuals was low (0.43%) (Higgins *et al.* 2000). Compared to areas burnt less frequently, areas burnt more frequently had significantly more short woody individuals. The low mortality rate and the dominance of shorter individuals may indicate an active “gulliver” syndrome (Higgins *et al.* 2007). The “gulliver” syndrome means that individuals may exist for long periods by resprouting after fires, and although short, they may be advanced in age (Bond and van Wilgen 1996, Higgins *et al.* 2000). This finding was supported by the significantly higher proportion of resprouting individuals in areas burnt more frequently in the old field grasslands. Therefore, the prediction that frequent fires would reduce the height of woody plants, according to the Higgins *et al.* (2000) disturbance model, was correct in the old field grasslands.

The prediction that solitary/unclustered macrophyllous woody plant species would be more pyrophobic than microphyllous woody plant species was supported by this study. Vegetation composition was significantly affected by fire frequency. The low density of macrophyllous woody species (e.g. eucleas such as *Euclea schimperi* and other species such as *Pappea capensis*) in areas with higher fire frequencies has been demonstrated elsewhere (Skowno *et al.* 1999, Gignoux *et al.* 2009). Importantly, these macrophyllous species have been observed to encroach savannas within a decadal time scale (Skowno *et al.* 1999, Bond and Archibald 2003).

The evergreen macrophyllous *Euclea* species that have been shown to be increasing in IGR by Wiseman *et al.* (2004) have a low palatability, due to the presence of naphthoquinones and triterpenoids (Hutchings *et al.* 1996), compared to deciduous microphyllous species such as *Acacia nilotica* and *A. gerrardii* (Watt and Breyer-Brandwijk 1962, Bertolli 2009). The release of these species from herbivory may accelerate their rate of encroachment (Wiseman *et al.* 2004). The suppression of fire has further enhanced the encroachment of these species in IGR. Smith and Goodman (1987) hypothesized that microphyllous woody species act as nurse plants for macrophyllous woody plants (Smith and Goodman 1987). Smith and Goodman (1987) found that macrophyllous evergreen woody species (e.g. *E. divinorum* and *E. natalensis*) were limited to establishing in the shade of the dominant

deciduous microphyllous tree canopies (e.g. *A. nilotica*). Therefore, the shade provided by the dominant microphyllous woody plants was hypothesized to facilitate or “nurse” the development of evergreen macrophyllous thickets (Smith and Goodman 1987). By reducing the population densities of palatable microphyllous woody plants, elephants were predicted to reduce the number of “nursing” sites for the germination and development of macrophyllous woody plants. Therefore, Smith and Goodman (1987) asserted that elephants may limit the encroachment of macrophyllous woody plants. Skowno *et al.* (1999) demonstrated that not all macrophyllous woody plants required microphyllous nurse plants. Therefore, elephants may not control the invasion of macrophyllous woody plants as Smith and Goodman (1987) described. In fact, elephants by themselves are ineffective at opening closed woodlands or forests, but instead have been known to maintain shrublands (Kalwij *et al.* 2010, Midgley *et al.* 2010). However, fire and elephants working together may facilitate the reversion of dense woodlands to more open savannas (Dublin, 1994, Midgley *et al.* 2010).

Management recommendations and further research

For the effective use of fire in IGR, management should act to optimize grass vigour or fuel load. To achieve this, the temporal and spatial extent of fires must be considered. For example, a small area burnt far from other nutritious forage would attract a high concentration of herbivores (Archibald *et al.* 2005). Therefore, the negative impact of herbivores on grass vigour would be concentrated in a few small areas (van Langevelde *et al.* 2003, Archibald *et al.* 2005). To avoid the increased negative impact of localised high densities of herbivores on grass vigour, fire must be used carefully to spread the impact of grazing herbivores (Archibald *et al.* 2005). A sufficient rest period is also required for the maintenance of a healthy grass sward (Trlica and Rittenhouse 1993). The population numbers of overstocked grazing herbivores must also be appropriately reduced (van Rooyen and van Rooyen 2008). The application of these factors to optimize grass vigour would allow sufficient fuel for intense fires (where possible) that are required to assist in the control of bush encroachment.

Regarding fuel loads, future research needs to focus on the factors that affect fuel load accumulation. Notably, research needs to determine the factors that affect grazing herbivore distributions, e.g. differences in soil properties. This would be achieved by monitoring herbivore movements at a number of sites with different topographical and edaphic variables as treatments. The proximity of the test sites to water would also have to be considered (Thrash 1998, Chamaillé-Jammes

et al. 2007, Matchett 2010). The construction of a number of grazing enclosures would help determine what woody plant species are influenced by herbivores.

To control the encroachment of microphyllous woody species in IGR, intense fires (where possible) should be used at an intermediate fire frequency (one burn every 2 to 4 years). In IGR, my field surveys indicated that fires were not hot enough to control encroaching species, particularly in the old field grasslands. Failing the use of intense fires at an intermediate fire frequency, the rate of woody plant encroachment in IGR will likely increase. Encroaching microphyllous woody species, once established, would suppress the grassy layer (van Langevelde *et al.* 2003). The suppression of the grassy layer would result in inadequate fire frequencies and intensities and may allow the invasion of macrophyllous woody species. The development of macrophyllous thickets would further suppress the grassy layer, increasing the resilience of these patches to fire (Skowno *et al.* 1999, Hoffmann *et al.* 2003, Gignoux *et al.* 2009). The dividing of the grassy layer by macrophyllous thickets would decrease the effectiveness of fire over the landscape, extending the longevity of these thickets (Hobbs 1996, Hoffmann *et al.* 2003).

The harvesting or slashing of encroaching woody plants is another option that has been used successfully to maintain open savannas (Pratt and Knight, 1971). This may be particularly useful in areas where fire can no longer be used (e.g. eroded sites or areas with poor fuel load accumulation) or is too dangerous to use, e.g. close to tourism infrastructure. By reducing the density of encroachers using this method, the productivity of the herbaceous layer can be expected to increase (van Langevelde *et al.* 2003). Therefore, with increased fuel loads the effectiveness of fire may also increase following the manual removal of encroaching trees.

Regarding fire, future research needs to assess the factors that may cause the reversion of closed woodlands and macrophyllous thickets to more open savannas. Such an opportunity may present itself in the accidental event of a canopy fire (Ikeckukwu Muoghalu 2006). The documentation of the secondary succession of woody and herbaceous plants after such an event may be invaluable. Canopy fires, that are caused by intense grass fires (Trollope *et al.* 2002), can be dangerous to human life (Bond and Archibald 2003) and have been avoided by IGR management. In the past, canopy fires may have been more frequent and important in controlling the spread of macrophyllous thickets. An accidental canopy fire may be crucial in maintaining an open savanna area and prevent the loss of biodiversity to bush encroachment (Asner *et al.* 2004, Ward 2005).

There was inconsistent evidence for the role of global climate change on the vegetation of IGR. Controlled glasshouse experiments have suggested that woody plant competitive ability increases with increasing CO₂ levels. However, field studies have not found sufficient evidence relating bush encroachment to increasing CO₂ levels (Archer 1995, Körner *et al.* 2005, Stock *et al.* 2005). I found a decrease in lighter rainfall events (5 – 10mm) and increase in higher rainfall magnitude events (>20mm), which can be associated with climate change (Smakhtina 1998, Benhin 2006), and may facilitate the encroachment of woody plants (Knoop and Walker 1985). Future research needs to determine the effects of these changes in rainfall patterns by simulating these rainfall events in the field, similarly to Knoop and Walker's (1985) experiments. These experiments would demonstrate which encroaching species are likely to encroach with changing rainfall patterns, as well as guide future management decisions.

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