

UNIVERSITY OF KWAZULU-NATAL

THE ROLES OF COMPETITION, DISTURBANCE AND
NUTRIENTS ON SPECIES COMPOSITION, LIGHT
INTERCEPTION AND BIOMASS PRODUCTION IN A SOUTH
AFRICAN SEMI-ARID SAVANNA

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The roles of competition, disturbance and nutrients on species
composition, light interception and biomass production in a
South African semi-arid savanna

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PREFACE

The experimental work described in this thesis was carried out by Keletso Mopipi in the School of Biological and Conservation Sciences University of KwaZulu-Natal, Pietermaritzburg, and at the University of Fort Hare, Alice, from October 2006 to June 2009 under the supervision of Professor Kevin Kirkman.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

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GENERAL ABSTRACT

Plants are the major source of food or energy required to sustain life on the planet, but humans are grappling with the deteriorating conditions of natural ecosystems such as compositional change, desertification, invasive plants and soil erosion. In the face of global climate change and growing demands for agricultural productivity, future pressures on grassland ecosystems will intensify, therefore sustainable utilization of all plant resources is of vital importance to enhance food security within the limits of good conservation. The semi-arid grasslands of southern Africa represent major grassland resources for grazing. Herbage production in these areas is determined not only by water and nutrient availability, but also by controlled and uncontrolled fires. Since fire is regarded as a natural factor in savannas, it is essential to develop a deeper understanding of the role of fire in community structure and function for the development of appropriate burning regimes. A study was conducted in the Eastern Cape of South Africa where the rural communities are faced with the challenges of rangeland degradation in the form of encroachment by unacceptable bush, karroid, macchia and less desirable grass species, as well as soil erosion. The main objective of this thesis was to investigate the roles of competition and disturbance regimes (fire and simulated non-selective grazing) on species composition, habitat productivity and the performances of selected species from this semi-arid savanna.

Long-term effects of burning frequency on herbaceous species composition, Leaf Area Index (LAI), Photosynthetically Active Radiation (PAR) within the herbaceous canopy, biomass production and soil chemical properties were investigated. These studies were conducted on a fire trial set up in 1980 at the University of Fort Hare research farm in the Eastern Cape, South Africa. The treatments comprise an annual, biennial, triennial, quadrennial, sexennial and no burn control, all replicated twice in a Complete Randomized Design. The data from the trial collected between 1980 and 2008 were used to determine compositional variation for herbaceous species using the Non-metric Multidimensional Scaling and Bray-Curtis Dissimilarity tests. The PAR ceptometer was used to determine LAI and intercepted PAR, while random samples were harvested from 1m² quadrats from each plot. Soil samples were taken at four depths (0-2 cm; 2-4 cm; 4-6 cm and 6-8 cm) from each plot and analyzed for pH, Ca, K, P, total C and total N. The Resin-Bag technique was used to determine nitrogen mineralization.

Burning frequency caused significant variation in herbaceous species composition over time. The species were distributed along gradients of increasing burning frequency, and these responses were in three categories: Those that increased with burning frequency such as *Themeda triandra*; those that decreased with burning frequency such as *Melica decumbens*, and those that showed little response such as *Panicum maximum*. The three-year burn resulted in the highest compositional variation, light interception, Leaf Area Index, aboveground biomass production, while the annual, biennial and no burn treatments resulted in the lowest. The fact that infrequent burning resulted in higher species variation, improved habitat productivity due to increased leaf area for light interception shows that appropriate use of fire can maintain a more diverse and productive savanna system. Burning frequency had significant effects on the soil properties, while soil depth did not show any significance. Frequent burning increased soil pH, K, Ca, and Na, but reduced C, N, P and N mineralization. There was a negative correlation between burning frequency and N mineralization, but no correlation existed between N mineralization and total N, total C or the C:N ratio. These results imply that frequent burning can cause nutrient losses and a greater nutrient limitation to plants in the long-term, especially soil C and N loss from combustion of organic material in the soil top layer.

The ability of shade-tolerant plants to persist under shade and regular defoliation such as in burnt and grazed systems may be of greater importance for long-term productivity and sustainability of forage crops. It is therefore imperative to explore the mechanisms by which some species were favoured by frequent burning which created low shade conditions, while others were favoured by high shade conditions where burning is infrequent or absent. A pot experiment was conducted to investigate the shade tolerances of seven grass species that were abundant in the long-term fire trial. The test species were *Cymbopogon plurinodis*, *Digitaria eriantha*, *Eragrostis curvula*, *Melica decumbens*, *Panicum maximum*, *Sporobolus fimbriatus* and *Themeda triandra*. Individual grass tillers of each species were collected from the natural vegetation, propagated in separate seedling trays and transplanted into individual pots, and were grown under five shading treatments: full sun (0 % shading), 55 %; 70 %; 85 % and 93 % shading respectively. Shading significantly reduced the dry matter production of all the species. Biomass production of all the species decreased linearly to varying degrees with an increase in shade intensity. *Digitaria eriantha* and *Eragrostis curvula* were most adversely affected by shading, hence are classified as shade intolerant, while *Melica decumbens* was the

least affected by shading, and is hence classified as shade tolerant. *Cymbopogon plurinodis*, *Panicum maximum*, *Sporobolus fimbriatus* and *Themeda triandra* are classified as moderately shade-tolerant. From the results it was apparent that some species could perform optimally in partial shade than in full sunlight, and these results lead to a conclusion that for satisfactory natural regeneration and seedling growth of this savanna vegetation would require a gap large enough to provide at least 30 % of ambient light.

Investigating patterns in competitive effects and responses of species in these communities may not only explain the abundance of each species, but may also provide insight into the nature of forces that affect the structure and function of that community. Since fire, herbivory and soil nutrients are natural drivers of savanna community structure and function, their influence on competitive interactions of selected species were investigated. Two experiments were conducted to investigate the competitive effects and responses of eight selected common species in the area. The test species (phytometers) included one woody shrub, *Acacia karroo* and seven grass species namely: *Cymbopogon plurinodis*, *Digitaria eriantha*, *Eragrostis curvula*, *Melica decumbens*, *Panicum maximum*, *Sporobolus fimbriatus* and *Themeda triandra*. In an outdoor plot experiment the responses of the phytometers to competition from neighbours (0; 2 and eight neighbours respectively), fertility (fertilized, unfertilized) and clipping (clipping, no clipping) were investigated. The second comprised a pot experiment where the competitive effects of the species were investigated. Each species was grown under 3 levels of fertility (0 %; 50 % and 100 % Hoagland's solution) and clipping (clipping, no clipping) in pots filled with fine river sand and 4 neighbours. Competition intensity, soil fertility and clipping had significant effects on the biomass production of the phytometer species. *Acacia karroo* and *Melica decumbens*, exhibited the weakest competitive effects and responses, and incurred the highest mortalities after clipping and with 8 neighbours. *Digitaria eriantha* and *Panicum maximum* exhibited the strongest competitive effects and responses, especially in high fertility, and experienced the lowest mortalities. *T.triandra* exhibited stronger competitive effect after clipping in low fertility, while *A. karroo* and *C. plurinodis* exhibited stronger competitive effects in moderate (50 %) fertility. *Cymbopogon plurinodis*, *Eragrostis curvula* and *Sporobolus fimbriatus* ranked between these two extreme groups in terms of competitive effects and responses. Relative Competitive Interaction increased with soil fertility and number of neighbours in the absence of clipping. These results indicate that in general, taller or broad-leaved grass species outgrow the shorter ones, and this gives them a competitive advantage over light and soil resources.

One of the range management objectives in the False Thornveld of the Eastern Cape is to promote the abundance of *Themeda triandra*, which is of high forage value and an indicator of rangeland that is in good condition. The general situation under livestock farming conditions in this area is that if the grass sward is optimally grazed and rested then there is a great potential for *Themeda triandra* to dominate. The results of the competition experiments indicated that the species exhibits strong competitive interaction, and also exhibited stronger competitive effect after clipping in low fertility. These results imply that it has a low response and a high effect, an attribute that would enhance its performance if it is moderately grazed or the area is burnt. The species is also moderately shade tolerant, and this may explain why it thrives in burnt and moderately grazed areas.

These studies have demonstrated the important role that competition and disturbance in the form of fire and herbivory play in the maintenance of this savanna grassland. Through natural selection species are able to occupy different niches in the same area and coexist in a heterogeneous environment and minimize their chances of extinction.

Keywords: Biomass production, competition, fire frequency, light interception, Leaf Area Index, nitrogen mineralization, plant community, savanna grassland, shade tolerance, soil nutrients.

DECLARATION 1 – PLAGIARISM

I, Keletso Mopipi 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.
4. This thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
 - a. Their words have been re-written but the general information attributed to them has been referenced.
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5. This thesis does not contain text, graphics tables copied and pasted from the internet, unless specifically acknowledged, and the source being detailed in the thesis and in the reference sections.

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LIST OF SYMBOLS

CV = Coefficient of Variation

FAO = (United Nations') Food and Agricultural Organization

UNESCO = United Nations Educational, Scientific and Cultural Organization

fIPAR = Fraction of Intercepted Photosynthetically Active Radiation

FORIG = Forestry Research Institute of Ghana

IPAR = Intercepted Photosynthetically Active Radiation

LAI = Leaf Area Index

LCP = Light Compensation Point

LMA = Leaf Mass per Area

NAPP = Net Aboveground Primary Production

NPP = Net Primary Productivity

NMS = Nonmetric Multidimensional Scaling

PAR = Photosynthetically Active Radiation

RH = Heterotrophic respiration

SOM = Soil Organic Matter

Species' names

AKKAR = *Acacia karroo*

CYNDA = *Cynodon dactylon*

CYMPL = *Cymbopogon plurinodis*

DIGER = *Digitaria eriantha*,

ERCUR = *Eragrostis curvula*

ERCL = *Eragrostis chloromelas*

ERAOB = *Eragrostis obtusa*,

EUSMUT = *Eustachys mutica* (name changed to *Eustachys paspaloides*)

HETCON = *Heteropogon contortus*

KAR = All Karroid species

MELDE = *Melica decumbens*

MICAF = *Microchloa caffra*

PANEQ = *Panicum aequinerve*

PANMAX = *Panicum maximum*,

PANSTAP = *Panicum stapfianum*

SPOAF = *Sporobolus africanus*

SPOFI = *Sporobolus fimbriatus*

THTRI = *Themeda triandra*

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DEDICATION

I would like to dedicate this thesis to my late mother, mme Sennyatseng Mmemme Hildah Marumo, whose inspiration and unconditional love kept me going even when the road seemed bleak. You have inspired me to persevere and strive to complete these studies. Mum, you will always be loved, cherished and remembered for the contribution you made to our individual lives, family, children and society at large. May your humble soul rest in paradise.

CHAPTER 1 GENERAL INTRODUCTION

1.1 The structure and function of ecological systems

Ecosystems are dynamic, complex and composed of many interacting parts. Systems have unique characteristics (emergent properties), which are only manifest when sub-components interact to larger functional wholes (Briske et al. 2005). Due to the complexity of ecological systems, their organization can be best understood when viewed as a graded series with several levels of organization such as populations and communities, referred to as the hierarchy theory (Russell, 1998). Each level of organization has its own characteristic properties that operate at different spatial and temporal scales (Archer et al. 2004). The abiotic and biotic components of ecological systems interact and are dependent on one another for the flow of energy and nutrient cycling as illustrated in Table 1.

Table 1 Generalized description of the structure of ecological systems. The abiotic (non-living) component comprises the chemical and physical environment of the biotic (living) component. (From Briske and Heitschmidt 1991).

Structure of Ecological systems	
<u>Abiotic component</u>	
Radiation	Soils
Climate	Geography
Atmosphere	Fire
<u>Biotic component</u>	
<u>Organism</u>	<u>Function</u>
Plants	Producers } Autotrophs
Herbivores	Primary consumers
Carnivores	Secondary consumers
Decomposers	Primary, Secondary and Tertiary consumers
	} Heterotrophs

Plant species composition and productivity within a region largely reflect the prevailing climatic conditions, while seasonal and annual rainfall and temperature play an important role in dictating

population dynamics over time (Crawley 1997; Wright and Coleman 1999). However, substantial spatial and temporal variation occurs across landscapes, of which broad-scale climatic variables cannot account for the spatial patterns that shape vegetation form and function on a local scale. The study of individual organisms in ecological systems does not reveal the unique properties that emerge from interactions of organisms with each other and their environment at higher levels of organization (Begon et al. 1996). Studies at an individual plant level do not take into account the key processes operating at the community level of organization, but provides mechanistic explanations and insights to how systems work (Archer et al. 2004). Research at higher levels of organization should therefore be directed at not only understanding the behaviour of ecological systems at various levels of organization and ascertaining their emergent properties, but also the processes and mechanisms underlying the processes and inputs that regulate these key properties.

If the structural and functional aspects of ecological systems are to be understood at spatial and temporal scales appropriate for productivity and conservation, key plant and population processes must be identified and linked across time to community and landscape levels of integration (Archer et al. 2004). This is carried out using models, which are defined as systems of concepts, generalizations, or assumptions (Westoby et al. 1989). The model guides what data are collected, and how that information is assembled to arrive at management decisions. Rangeland management is commonly based on traditional succession models which imply that the replacement of one type of plant cover by another is a way to detect overgrazing and grazing value of a range site. There is an apparent weakness with the traditional approach, for example vegetation changes in response to grazing are often inconsistent or irreversible (Westoby 1980). The inability of the succession models to incorporate multiple pathways of change has led some ecologists to abandon the traditional theories of plant succession which lead to single climax communities (Smith 1989).

Plant species evolved towards a pattern of resource allocation which minimizes their chances of extinction. Such patterns have been retained and refined through the process of natural selection. The resource allocation pattern of a species determines, in part, its functional address (niche) in a community (Hartvigsen 2000). Natural ecosystems are heterogeneous, and more often than not, resources are in short supply consequently, competition becomes vital for fitness. Disturbance is recognized as an important factor affecting competitive interactions in South African grasslands and savannas (Fynn et al. 2004; Bond and van Wilgen 1996; van Wilgen et al. 2003) and across the globe (Begon et al. 1996; Tillman 1982; Keddy, 1989).

Equilibrium and non-equilibrium models have been proposed to try to explain competitive interaction in plants. Equilibrium models assume that plants make some trade-offs in competitive ability between their disturbed and undisturbed environments (Fynn et al. 2004). If communities are non-equilibrium assemblages, then the maintenance of species richness is dependent on dispersal and chance events (e.g. disturbance) and local selection on individuals (Hartvigsen, 2000; Freckleton and Watkinson 2001). In this case, disturbance reduces the intensity of competitive interactions, which reduces the ability of strong competitors to exclude weaker species (Fynn et al. 2004). This apparent controversy in the understanding of competitive interactions on plant community dynamics and the relevance of these models to observed changes in South African ecosystems necessitates more work to get a clearer understanding of the underlying mechanisms that promote those changes.

If the structural and functional aspects of ecological systems are to be understood at spatial and temporal scales appropriate for productivity and conservation, key plant and population processes must be identified and linked across time to community and landscape levels of integration (Archer et al. 2004). At this level of organization, effects of disturbance on microclimate, hydrology, energy flow, nutrient transformation and translocation, and soil physical/chemical properties operate against a backdrop of climatic variability to influence plant species interactions and cause fluctuation, retrogression and succession in plant communities (Wright and Coleman 1999). Fire is one of the most important disturbances in grasslands and savannas, and significantly affects vegetation cover, soil and biodiversity at decadal to centennial scales (Pausas 2006; Baeza et al. 2007). Fire is commonly used as a management tool for range and conservation purposes in these areas. However, its effects on vegetation, energy flow, hydrological and soil properties are not well understood by farmers and landowners in the Eastern Cape of South Africa. This is evidenced by the fact that some landowners are completely against controlled burning, while others apply it when it is recommended. This scenario necessitates further investigation because fire has a potential to improve forage production for grazing ungulates in rangelands, (Mapiye et al. 2008), while inappropriate use of fire leads to accelerated soil erosion and nutrient loss, loss of forage, adverse changes in species composition, increased undesirable herbaceous and woody species and consequently decreased animal performance (Trollope 1999).

1.2 Factors affecting composition and primary productivity in ecological systems

1.2.1 Solar radiation

The capacity of ecological systems to produce biomass could appear limitless due to the enormous and continuous flow of solar energy. However, above-ground primary productivity (usually expressed as plant growth/area/time), and subsequently secondary productivity (animal growth/area/time), are limited by two general categories of ecological constraints: The quality and quantity of solar radiation available for photosynthesis, as well as the occurrence of abiotic factors (such as water, temperature and nutrient limitations), limit solar energy capture from being maximized (Begon et al. 1996; Briske and Heitschmidt 1991). Primary production decreases mainly because of reduction in the availability of leaf area to intercept solar energy (Briske and Heitschmidt 1991), and this is very common in grazed and systems. In light of this, plant consumption by herbivores introduces an additional feeding level between the primary producers and decomposers, and therefore there is a need to understand how grazing influences energy flow and nutrient cycling in ecological systems.

1.2.2 Soil fertility

Plant growth is dependent on a favourable balance or a combination of light, mechanical support, temperature/heat, air, water and nutrients and except for light, soil is an agent in supplying wholly or part of all these factors (Buckman and Brady 1960; Killham, 1995). Soils and topography exert a strong influence on patterns of plant distribution, growth and abundance over the landscape through regulation of the plant available moisture from precipitation, which also affects nutrient availability (Killham 1995; Russell 1998). Influences of disturbances are superimposed on the background of this topo-edaphic heterogeneity and climatic variability to further influence community-level processes. As a result, species whose adaptation to the prevailing climatic conditions and soils is superior would make them the competitive dominants of the community under certain conditions of light and moisture (Archer et al. 2004). Silvertown (et al. 1999) highlighted that hydrologically defined niches reveal a basis for species richness in plant communities, and this demonstrates the importance of moisture on plant community structure.

1.2.3 Plant Competition

One of the biggest problems facing rangeland managers in many ecological systems is habitat degradation and compositional change, but the underlying mechanisms of these dynamics are not

well understood. Ecologists agree that competition often has a major role in structuring plant communities (Begon et al. 1996; Crawley 1997; Goldberg 1996; Grime 1977; Tilman 1982), hence the relationship between individual plant traits and competitive success in communities is an essential component of modelling the role of competition in structuring plant communities. Plants compete for both aerial resources (light) and soil resources (water and mineral nutrients). Since each ecological system has its own emergent properties, system-specific experimentation and modelling could provide deeper understanding so as to make more informed management decisions for optimum and sustainable utilization.

1.3 The effect of disturbance on ecosystem function based on Terrestrial Ecosystem Models (TEM)

Disturbances have been defined as destructive events and environmental fluctuations that cause change in conditions of an ecological system (White and Pickett, 1985). These are process which can change plant species composition by increasing the abundance of tolerant species at the expense of intolerant ones, and also improve light penetration for terrestrial plant seedlings (Tillman, 1982). Disturbances may either be intrinsic or extrinsic, or vary in duration, intensity, directionality and recurrence. Some intrinsic disturbances are driven by the life histories of the major species whose establishment, growth and subsequent death can create a shifting mosaic of species composition and the resultant trophic processes (McNaughton, 1992), while extrinsic factors such as catastrophic wildfires, windstorms or floods may drive other disturbances. However, some ecological systems are complex, dynamic ecological systems whose genesis and organization are fundamentally driven by disturbance regimes. Savanna and grasslands are characterized by recurrent, human-generated disturbances and also occur in regions where the climate is spatially and temporally variable (McNaughton, 1991). Therefore precipitation and the resultant composition and primary productivity vary significantly in space and in time.

The concept of non-equilibrium succession had its beginning in the earlier works of Watt (1947) and Raup (1957). These authors suggested that which ecological community occupies a site following a disturbance is determined by the severity and frequency of disturbance with potential for establishment of alternate communities (Connell and Slather 1977). In the absence of disturbance, the annual carbon exchange between an ecosystem and the atmosphere is the difference between net primary production (NPP), which represents the annual net carbon uptake

by the vegetation, and heterotrophic respiration (RH), which represents the carbon lost from the soil via microbial decomposition (Field et al. 2004). During succession, NPP gradually increases with the accumulation of vegetation carbon and heterotrophic respiration (RH) initially decreases because of a lower rate of inputs of dead organic matter into the soil. Eventually NPP becomes greater than RH at which time the ecosystem goes into positive carbon balance. In the absence of disturbance, RH rises as inputs to the soil rise and NPP gradually decreases until the carbon balance of the ecosystem is in equilibrium (Field et al. 2004). Fire and herbivory are the most common and often inevitable forms of disturbance in grasslands and savannas, and their role in plant community structure and competitive interactions will be investigated in these studies.

The fundamental relationship between the biodiversity of natural and modified environments and their net primary production has been a topic of significant scientific controversy and scrutiny. Early theoretical and empirical results indicated that production was sometimes significantly correlated with species richness when species richness was directly manipulated in experimental systems (Drake 2003). The size of a disturbance regime linked to successional process affects diversity (Connell and Slatyer 1977). In other words, small scale disturbances are important in fine scale niche differences and support species diversity. There may be a large amount of seed in the seed bank waiting for a chance to germinate. Disturbance also creates opportunities (chance) or opens niches for more marginalized species to successfully establish themselves.

Fire is widely accepted as an ecosystem driver in grasslands and savannas. The effect of fire on natural ecosystems involves the response of living organisms to the release of heat through the combustion of plant material (Bond and van Wilgen 1996; Trollope 2007), and this depends on type, intensity and season of burn (Teague and Smit, 1992; Trollope and Potgieter 1985). It has been described as a large generalist herbivore (Bond 1997), which sometimes competes with, sometimes replaces and sometimes facilitates herbivory (van Wilgen et al. 2003). Effects of fire on plant communities include persistence or tolerance by sprouting from dormant buds after a fire. Fire also influences recruitment, and some species have a near obligate dependence on fire for recruitment, while others respond to other cues for recruitment (Bond and van Wilgen 1996). These effects affect species diversity and productivity in South African savannas and grasslands, and hence their diversity and productivity. Fynn (et al. 2004) observed that grass species richness declined considerably in the absence of fire while forbs were unaffected, while annual burns without mowing increased grass species richness.

Succession and competitive interaction play integral roles in maintaining a desirable rangeland condition (Tow and Lazenby 2001), and in many parts of Africa, these concepts are not well documented. Inappropriate range management which often results from poor understanding of the factors which drive these systems such as climate and disturbance, has resulted in rapid change and habitat deterioration. Species composition and productivity are the key functional characteristics for animal production, of which competitive interaction is greatly influenced by disturbance in the form of fire and herbivory. Population dynamics models have been modified to interpret changes in fire prone plant communities and predict the outcomes of different types of fire on plant populations (Bond and van Wilgen 1996; Trollope 2007).

1.4 Problem statement and justification for the studies

Natural, semi-natural and artificial grasslands and savannas are highly dynamic ecosystems that support flora, fauna and human populations worldwide. These areas cover approximately 40 % of the terrestrial land surface (Bailey, 1996), account for about 35 % of net primary productivity (Field et al. 1998) contain about 20 % of the world's human population and support the majority of the world's livestock (Archer et al. 2004; Turner et al. 1990). They provide goods and services such as food, energy, biodiversity conservation, carbon storage, tourism, and habitats for endemic bird and wild herbivore species. In South Africa, these systems are important in agriculture, conservation, rural livelihood and tourism (Chirara 2001; Kranz 2001; Scogings 2003; Scholes and Walker 1993; Young and Solbrig 1993). As mentioned by Watkinson and Ormerod (2001), in the face of climate change and growing demands for agricultural productivity, future pressures on grassland ecosystems will intensify. It is clearly apparent that sustainable utilization of these systems is of vital ecological and socioeconomic importance.

Successful management of valued biota for both productivity and conservation poses several dilemmas for farmland managers and conservationists, and these calls for improved understanding of the relevant applied ecology. One of the biggest problems facing rangeland management in many ecological systems is habitat degradation and compositional change. Although pivotal in grassland management, poor predictive understanding of the causative factors and underlying mechanisms of change creates a deficiency for present and future research. Grazing-induced modifications in species composition have been documented in many parts of the world and these

often involve replacement of species occupying higher succession seres by lower succession species (Westboy 1980; Smith 1989; Tow and Lazenby 2001; Walkinson and Ormerand 2001).

Traditionally, disturbances caused by fire, insects, disease, drought and wind were considered destructive, but these have recently come to be regarded as key to ecological processes in succession of ecosystems (Bond and van Wilgen 1996). A number of models have been proposed to explain the role of various disturbance regimes on plant community dynamics since the early twentieth century. Clements (1928) proposed a model in which climate was the determining factor, and the community a reflection of that climate. Substrates were of minor importance in the replacement of higher life forms as the community moved toward a stable climax stage, and disturbance was viewed only as an interruption of succession toward equilibrium with the regional climate. The effects of disturbance regimes in structuring plant communities gained greater significance with further studies of succession in terrestrial systems (Pickett 1980; White 1979). Pickett (1980) considered competitive exclusion as the driving mechanism moving succession toward equilibrium community, while White (1979) noted that forest communities seldom reached competitive exclusion stage, becoming more susceptible to disturbance with age. Therefore, as Cahill Jr. (2002) highlighted, examining the effects of disturbance and competition on species diversity and habitat productivity offers further insight into differentiating alternative models of plant community organization.

Livestock production contributes significantly to the livelihoods of rural people in South Africa. Of the approximately 14.1 million cattle in South Africa, 3.1 million are found in the Eastern Cape Province (National Department of Agriculture 2008), and about half of these belong to communal farmers (Ainslie et al. 2002). Improving livestock production to reduce poverty and increasing food security in these areas would entail good rangeland management practices to increase forage production and reduce rangeland degradation. The use of fire as a range management practice is one of the topics of debate that needs to be addressed, as well as grazing systems. Experiments in the semi-arid savanna called the 'False Thornveld of the Eastern Cape' have suggested that controlled burning (compared with bush cutting, chemical application, etc.) may be the most appropriate way of increasing primary production of herbaceous species (Trollope 1983; 1999), which is essential for increasing the grazing capacity in that pastorally important region. The effects of fire on species composition and primary productivity were examined at the University of Fort Hare research farms to understand the mechanisms involved. Recommendations from this

research would contribute towards appropriate predictions concerning sustainable management plans of South African grasslands and savannas, and the Eastern Cape Province in particular. Grazing has traditionally been perceived to have a negative impact on the subsequent rate of energy capture and primary production through direct and indirect effects on plant growth (Briske and Heitschmidt 1991). Its effect on competitive effect and responses of key grass species will also be investigated.

1.5 Main objectives of the studies

This research is aimed at determining and understanding the role of disturbance regimes and competition on plant community structure and function of savanna grassland. The specific objectives of the studies are as follows:

1. To determine the long-term effects of long-term burning frequency on species composition of savanna grassland;
2. To investigate the role of fire on light availability and habitat productivity;
3. To determine the effect of long-term burning frequency on soil nutrients;
4. To investigate the shade tolerances of selected key grass species of a savanna grassland;
5. To compare the competitive effect and response hierarchies of key grass species of a savanna grassland along gradients of soil fertility and simulated non-selective grazing.

The outcome of this research would contribute to the knowledge base to develop an understanding of the underlying mechanisms driving succession in rangelands in semi-arid arid grasslands and savannas. This will contribute towards developing adaptive range management and conservation programs to control compositional change, conserve biological diversity and reduce rangeland degradation in the grazing areas of the Eastern Cape.

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CHAPTER 2 LONG-TERM EFFECTS OF FIRE FREQUENCY ON HERBACEOUS SPECIES COMPOSITION IN A SOUTH-AFRICAN SAVANNA

Abstract

The long-term effects of burning frequency on herbaceous species composition were examined in semi-arid savanna vegetation near Alice, a small town in the Eastern Cape Province of South Africa. The trial was established in 1980 and treatments comprise an annual, biennial triennial, quadrennial, sexennial early spring burns and a no burn treatment, each with two replications in a Completely Randomized Design. Species composition was determined each year before burning, and the data collected between 1980 and 2008 was used in this study. A total of 20 grass species, several forbs and karroid species were also recorded. Nonmetric Multidimensional Scaling and the Bray-Curtis dissimilarity tests were used to test for compositional variation between burning treatments over time. In general, compositional change increased with fire frequency. Species abundances and distribution were influenced by fire treatments over time, whereby individual species were dispersed along gradients of increasing/decreasing fire frequency, and these also varied with sampling year.

The triennial and quadrennial burns produced the longest NMS ordination distances between 1982 and 1983, signifying the highest magnitude of compositional change, which was also directional. These were followed by the no burn and sexennial burns, while the annual and biennial burns had the shortest ordination distances. *Themeda triandra*, a fire-tolerant species was most abundant in the annual, biennial and triennial plots, but gradually decreased with less frequent burning, while *Melica decumbens* was most dominant in the no burn and six-year burns, but gradually disappeared with increasing fire frequency. Several other species such as *Digitaria eriantha*, *Eragrostis species*, *Panicum stapfianum* and *Sporobolus africanus* were also abundant in most of the treatment plots. There was a highly significant variation in species abundances between 1980 and 2008 and the species abundances were also significantly influenced by burning treatments. The percentage dissimilarities for the annual and biennial burns (77.1 and 70.5 % respectively) were significantly higher than those of the triennial, quadrennial and sexennial burns respectively. The triennial and quadrennial burns exhibited the most diverse species composition after 28 years

of burning treatment, with the abundance of both fire tolerant and fire intolerant species. These two fire regimes appear to be the most suitable fire frequencies to apply when using fire as a management tool in this vegetation type where there is no grazing.

Keywords: Burning frequency, Bray-Curtis Dissimilarity, fire tolerant, Nonmetric Multidimensional Scaling, species composition.

2.1 Introduction

2.1.1 Fire as an ecological phenomenon

Fire is an important phenomenon of the natural world, an agent of change that performs a variety of functions and produces a range of effects on vital attributes of plant species (Noble and Slatyer 1980), and consequently influencing other components of ecosystem functioning (Bravo et al. 2008). It causes changes in environmental conditions for plant growth and establishment, thus affecting plant community organization and biodiversity (Whelan 1995; Bond and van Wilgen 1996), as well as soil physical and biochemical properties (Clemente et al. 2005). Tropical and sub-tropical grasslands, savannas and forests are the main ecological systems where fire plays a central role in determining community composition, structure and function, and in shaping the life history characteristics of the component plant species (Trollope 1983; Snyman 2004; Boletta et al. 2006).

The disturbance of a plant community by fire generally results in a more xeric environment as well as increased tiller mortality, and in water limited environments, plant productivity in the first season after fire is generally reduced relative to pre-fire levels (Defosse and Robberecht 1996). Temperatures or heat shocks generated from fires however, are reported to play a role in releasing seed dormancy of legumes in arid and semi-arid regions (Cox et al. 1993; Kulkarni et al. 2007; Mbalo and Witkowsky 1997). Fire also breaks hard seed coat dormancy by the physical burning of the seed coat, resulting in an increased water intake and gaseous exchange, and this enhances seed germination (Mucunguzi and Oryem-Origa 1996). Smoke generated from fire plays an important role in the establishment and maintenance of many plant communities such as the Fynbos in South Africa (De Lange and Boucher 1990), Kwongan in Australia (Dixon et al. 1995), and the Mediterranean basin (Crosti et al. 2006).

Unlike other processes that threaten biodiversity, fire is an environmental factor that can threaten or benefit biodiversity depending on fire regimes (Trollope 1983; 1999). Fires can, on one hand, release essential elements such as phosphorus and potassium from plant organic matter back into the soil in the form of mineral-rich ash, which makes them readily available for plant absorption. On the other hand some elements, particularly nitrogen, could be lost to the system through volatilization during combustion. Due to its profound effects on the biotic and abiotic environment, fire has become a management tool in many areas where it is a system driver. Its uses generally

include land clearing, range management for livestock and game, protection of property, cultural and spiritual purposes and for biodiversity conservation (Setterfield 2002). The specific objectives for the use of fire vary from area to area, and they include eliminating litter, increasing forage production and quality, controlling undesirable plant species, altering botanical composition by maintaining fire-dependent species and keeping conservation areas pristine (Mentis and Bailey 1990; Malan and van Niekerk, 2005). The need for the understanding of fire ecology, which probes the relationship between fire and living organisms and their abiotic environment therefore, cannot be underestimated.

Prescribed burning, defined as ‘the use of fire of pre-set characteristics to achieve a specified change in a known plant community’ (Weekem and Strang 1983), is a well recognized practice for managing vegetation in southern Africa (Trollope, 2007; Snyman 2004). This definition implies that managers are knowledgeable about fire behaviour and its characteristics such that predictable results can be accomplished under a variety of weather and fuel conditions in a given area. This is not necessarily the case considering the devastating effects of human-induced uncontrolled fires that occur every year across the globe, as well as some controversies concerning the ecological consequences of its application on ecosystem function (Setterfield 2002). Hence the need to enhance the knowledge-base on fire effects, as well as the appropriate regimes characterizing those effects under various environmental conditions.

2.1.2 A brief overview of fire ecology

A few concepts provide the basis for fire ecology, and these include fire dependence, fire history, fire regime and fire tolerance or adaptation. The concept of fire dependence applies to species of plants that rely on the effects of fire to make the environment more hospitable for their regeneration and growth. Fire history describes how often fires occurs in a geographical area. Dendroecological studies can be used to study fire regimes (Bravo et al. 2008). Evidence such as the presence of fire scars, or a layer of charcoal remaining on a living tree as it adds a layer of cells annually, provide a record that can be used to determine when in history a fire occurred (Grau et al. 2003; Bravo et al. 2008; Vanniere et al 2008). Fire adaptation applies to species of plants that have evolved with some special traits contributing to successful abilities to survive fires at various stages in their life cycles. Examples include serotinous cones, fire resistant bark, stoloniferous or rhizomatous growth, fire resistant foliage, or rapid development and growth that

enable a variety of plants to survive in a fire prone environment (Peterson and Reich 2001; Snyman 2004).

Fire regime is a generalized description of various fire characteristics such as type of fire, fire intensity, frequency and season of burn and the vegetative community (Trollope 1983; Trollope 2007; Bond & van Wilgen 1996). In the arid savannas the frequency of fires has been far lower than in the moist savannas because the rainfall is both less and highly erratic, and the grass sward remains acceptable to grazing animals even when matured (Trollope 1983), thus reducing fuel load. The frequency of fire in the arid areas varies according to the prevailing conditions. Fire also affects the environment indirectly by removing or reducing plant and litter cover, thereby modifying both the post-fire microclimate and the activity of soil biota (Trollope 1983). In southern Africa the importance of fire as a driving variable in most of the vegetation system is well established (Snyman 2004). Fires in southern African savannas typically occur late in the dry season (August–November), prior to the first seasonal rains (Hudak et al. 2004). On the other hand, dominance of fire as a land management tool has resulted in many debates over the ecological consequences imposed by fire regimes (Setterfield 2002; Vannere et al. 2008), and these debates warrant long- term research to have more understanding of the role of fire on community dynamics.

2.1.3 Fire frequency and species composition

Fire frequency describes the number of fires experienced by a particular community within a given time period. It can potentially be expressed in terms of a number of interacting variables such as time since the most recent fire, the length of fire-intervals and the variability of the inter-fire intervals (Morrison et al. 1995). Increasing time since fire is associated with a decline in the evenness of fire tolerant species (Morrison et al. 1995). Thus it is related to a high abundance of the fire intolerant species which tend to dominate the community in the prolonged absence of fire. These scenarios show that species exhibit two forms of life pertinent to fire effects on vegetation: those which persist with frequent burning, classified as fire- tolerant (or fire-dependent), and those which do not persist under frequent fires, referred to as non-tolerant (fire- independent) species. Theory suggests that species richness should be highest at intermediate levels of disturbance (Uys, et al. 2004), but this is not always the case. In the Scottish Highlands, for instance, plant diversity increased with fire frequency, while in North American prairies, plant diversity decreased with

increasing fire frequency (Uys et al. 2004). In addition, Gary and Morrison (1995) also reported that short-fire intervals are associated with a reduction in the number of species present in the community. Prolonged absence of fire allows the herbs and small shrubs to decrease in abundance, while large shrubs increase in abundance (Morrison et al. 1995). In savannas of Southern Africa the exclusion of fire leads to bush encroachment, an increase in woody plant density, basal areas and canopy cover (Peterson and Reich 2001; Russel-Smith et al. 2003, Wiegend et al. 2006). Bush encroachment often results in the formation of impenetrable thickets, and a significant suppression of palatable grasses and herbs. Furthermore, the encroaching woody plants are often unpalatable to domestic animals. Controlled burning is therefore considered as one of the least capital intensive methods that can be used to control bush encroachment in grasslands and savannas.

Most frequently burned areas are characteristically lower in tree density than unburned areas, with annual and biennial burns producing the greatest reduction in canopy density (Peterson and Reich 2001). The main short term impact of fires is to prevent the replacement of herbaceous strata by woody biomass and to enhance the production of some graminaceous species (Bucini and Lambin 2002). High frequencies of fires have been credited with creating and maintaining savannas (Peterson and Reich 2001). Species richness generally increases with the longer fire intervals, but composition of grass species consistently changes as fire becomes more frequent (Uys et al. 2004). In the False Thornveld of the Eastern Cape frequent burning favours the dominance of the fire-tolerant *Themeda triandra*, but has a negative effect on the abundance of fire-intolerant species such as *Cymbopogon plurinodis* and *Melica decumbens*. *Themeda triandra* is reported to thrive under frequent burning, and this could occur because burning improves conditions for light penetration by removing litter and moribund grass and if there is poor light conditions, species such as *T. triandra* would perform lower than the more shade tolerant species such as *C. plurinodis*.

Trollope (1983) stated that when considering the effect of frequency of burning on vegetation, a clear distinction must be made between the effect of burning at a particular frequency, the number of times that the treatment has been applied and the type of management that is used during the interval between the fires. Furthermore, Trollope (1983) indicated that in the absence of grazing, annual burning result in a high rooted frequency of grasses but a low rooted frequency of forbs. In contrast, quadrennial burning caused a significant decrease in the grasses and a significant increase in the forbs. Factors such as overgrazing, drought and frost complicate the interpretation

of results ascribed to the response of the vegetation to a particular burning treatment (Trollope 1983). At Ukulinga farm, grass species composition was reduced by an absence of disturbance (fire/cutting), which supported the theory that disturbance, is necessary for maintaining species diversity (Fynn et al. 2004).

2.1.4 Justification for the study

Fire is an important management tool in rangelands and conservation areas of the Eastern Cape, but the fire regimes appropriate for controlled burning are poorly understood. In fact, the role of fire in maintaining rangelands has been misunderstood by the public in general; thus over time the use of fire has been noticeably reduced in many areas. For instance, Clover (2010) reported that burning of veld has been condemned by the general public as being a major cause of veld degradation and the resultant soil erosion. This is unfortunate because prescribed burning is an effective means of controlling selected unwanted and undesirable species in rangelands, and it also enhances livestock productivity (Mapiye et al. 2008). Therefore there is a need to investigate the effects of fire regimes (such as fire frequency) on important plant community attributes for more informed management decisions in these areas.

2.1.5 Objectives

This study was aimed at investigating the long-term effects of frequency of burning on herbaceous species composition of a semi arid savanna, in vegetation described as the ‘False Thornveld of the Eastern Cape’ (Acocks, 1975). The presence of long-term burning trials at Fort Hare research farm, as well as the availability of long-term data (collected since 1980) presented an opportunity for this study.

Specific objectives were:

- To determine long-term effects of varying fire frequency on herbaceous species composition
- To determine how fire frequency affects the abundances of selected key grass species of the False Thornveld of the Eastern Cape.

It was hypothesized that fire frequency would influence species composition by favouring fire-tolerant species under high burning frequencies and fire-intolerant species at lower frequencies according to individual plant history strategies, promoting maximum overlap of species at intermediate frequencies.

2.2 Material and Methods

2.2.1 Study site

The study was conducted at the University of Fort Hare research farm near Alice, in the Eastern Cape Province of South Africa (32° 47' S; 27° 01' E). The research farm is situated 80 km inland from the Eastern Cape coastline at an altitude ranging from 500 m to 620 m, and covers an area of 1600 ha. The burning trials were established in 1980 and the objective of the experiment was to determine the frequency of burn on species composition, forage production and basal cover.

2.2.2 Physical environment

The geology of Fort Hare research farm is varied, and the soils are generally regarded as fertile. The area is primarily characterized by patches of medium-textured shallow young soils. There are also some occurrences of moderate to deep and potentially productive soils in river valleys (Mandiringana et al. 1999; Scogings 1998). The soils are primarily of the Caledon type, comprising some mixed alluvial parent material. The majority of the soils are of the Hutton, Oakleaf and Westleigh forms and classified as *Oakleaf Caledon* according to the South African Classification System, or *Chromic luvisol* in the WRB (FAO) classification system (Mandiringana et al. 1999; Soil Classification Working Group 1991; Mopipi et al. 2009).

2.2.3 Climate and vegetation

The climate is primarily subtropical, but the area also experiences a wide variety of topographic and climatological conditions. It receives a highly variable annual rainfall (CV = 22- 27 %) of about 600 mm, 75 % of which falls between October and April in relatively few heavy downpours, and a pronounced dry winter season from May to August (Dziba et al. 2003; Scogings and Mopipi 2008). The mean minimum temperatures vary from 5 °C in July to 11 °C in January, and the mean maximums vary from 26 °C in July to 41 °C in January. The vegetation is a semi arid bush-clump savanna consisting of grassland, thickly interspersed with subtropical deciduous shrubs dominated by *Acacia karroo*, and was described by Acocks (1975) as the False Thornveld of the Eastern Cape. The perennial grass layer varies with soil type (Stuart-Hill and Tainton 1989), and common species include *Themeda triandra*, *Cymbopogon plurinodis*, *Panicum maximum*, some *Eragrostis* and *Sporobolus* species, *Digitaria eriantha*, forbs, sedges, and some karroid shrubs such as

Chrysocoma ciliata. Most of the grasses use the C₄ photosynthetic pathway. Much of this vegetation type is used mainly as communal rangeland for livestock production as crop production is limited by climatic, topographic and geological factors (Lent et. al. 2000). However, patches which occur on river valleys are more productive and are hence used for intensive production of maize, pumpkins, vegetables and fruits under irrigation. Prior to commencement of the long-term trial, the experimental site was used as a communal rangeland by neighbouring villages, but was contributed to the University of Fort Hare by the local communities. The burning history of the study area prior to commencement of the experiment was not available on records. This is not surprising because in semi-arid rangelands, it is often not necessary to burn since intensive grazing significantly reduces grass fuel load, in which case burning is not usually recommended.

2.2.4 Experimental design and treatments

The burning trial comprises twelve 50 m x 100 m plots arranged across a slope close to a river valley. There are six treatments comprising a no burn control, annual burn, biennial burn, triennial burn, quadrennial and sexennial burns, arranged in a randomized complete block design with two replications (Figure 1). The treatments are applied between mid-July and mid- August just after the first spring rains.



Figure 2. 1 Experimental layout for long-term fire trial at the University of Fort Hare research farm (Google Earth 2010, Europa Technologies).

Table 2. 1 Illustration of treatment application plan for the long-term fire trials in camp 22 at Fort Hare research farm

YEAR	BURNING TREATMENTS											
	I/B1	II/B1	I/B2	II/B2	I/B3	II/B3	I/B4	II/B4	I/B6	II/B6	IK	2K
1980	B	B	B	B	B	B	B	B	B	B	NB	NB
1981	B	B									NB	NB
1982	B	B	B	B							NB	NB
1983	B	B			B	B					NB	NB
1984	B	B	B	B			B	B			NB	NB
1985	B	B									NB	NB
1986	B	B	B	B	B	B			B	B	NB	NB
1987	B	B									NB	NB
1988	B	B	B	B							NB	NB
1989	B	B			B	B					NB	NB
1990	B	B	B	B							NB	NB
1991	B	B									NB	NB
1992	B	B	B	B	B	B	B	B	B	B	NB	NB
1993	B	B									NB	NB
1994	B	B	B	B							NB	NB
1995	B	B			B	B					NB	NB
1996	B	B	B	B			B	B			NB	NB
1997	B	B									NB	NB
1998	B	B	B	B	B	B			B	B	NB	NB
1999	B	B									NB	NB
2000	B	B	B	B			B	B			NB	NB
2001	B	B			B	B					NB	NB
2002	B	B	B	B							NB	NB
2003	B	B									NB	NB
2004	B	B	B	B	B	B	B	B	B	B	NB	NB
2005	B	B									NB	NB
2006	B	B	B	B							NB	NB
2007	B	B			B	B					NB	NB
2008	B	B	B	B			B	B			NB	NB
2009	B	B									NB	NB
2010	B	B	B	B	B	B			B	B	NB	NB

LEGEND: B1 = Annual burn
 B2 = Biennial burn
 B3 = Triennial burn
 B4 = Quadrennial burn
 B6 = Sexennial burn
 K = No burn

2.2.5 Determination of herbaceous species composition

Each year before burning, the step-point sampling method (Trollope 1986) was used to determine herbaceous species composition by calculating the relative abundances of the grasses, Forbs and Karroo species. The procedure involved recording the nearest species to the point of a metal rod located at 2 step intervals from each other. For each plot 200 plants were identified and recorded from each sample points. All the grass species were identified, while other herbaceous plants were grouped and recorded as either Forbs or Karroo species. For each of the 12 treatment plots, the abundances of each herbaceous species were calculated and expressed as percentages.

2.2.6 Data analysis

A distance-based multivariate technique called Nonmetric Multidimensional Scaling (NMS) was used to assess variation in species composition across the six fire treatments from 1980 to 2008. The NMS is a polar ordination method based on redundancy analysis that uses species abundances data to identify gradients of compositional change (Sagar et al. 2008; Anderson and Willis 2003), and is adjusted to focus on time-dependent treatment effects, as well as enabling a quantitative interpretation of treatment effects on individual species (Ilomets et al. 2010). The procedure was conducted using CANOCO 4.5 for Windows. To quantify compositional variation between the six burning treatments in 1980 and 2008, the Bray-Curtis dissimilarity coefficients were calculated between burnt plots and each of the two no-burn controls at the beginning of the experiment (1980) and in 2008. Although the no-burn treatment plots also experienced compositional change over time due to exposure to environmental variables, no-burn 1 was used as reference points to test the effects of burning treatments on species composition since there was no prior monitoring or baseline data prior to commencement of the experiment. The two no-burn treatments were also compared using the Bray-Curtis Dissimilarity test to test the degree of variation due to other environmental factors apart from burning.

2.3 Results

2.3.1 The Nonmetric Multidimensional Scaling (NMS) sample ordination

The ordination of the plots was achieved with a final stress of 0.148 after 27 iterations for the two-dimensional solution. According to the two axes of the two-dimensional NMS sample ordination, species composition over time differed with burning frequency (Figure 2.2). In general compositional change increased with fire frequency. Dimension1 of the NMS ordination explained 62.7 % of the compositional variation, and distributed the species according to gradients of burning frequency. The extreme right of the diagram was occupied by species occurring in the no burn controls, while those in the extreme left were mostly found in the frequently burnt plots, mainly the annual and biennial burns. Dimension 2 of the NMS ordination was related to other environmental factors influencing species performances, but not accounted for in the experiment. These could include factors such as slope, aspect or soil heterogeneity. Time after commencement of experiment also appeared to have had some effect, because most of the species noticeably occupied the upper half of the axis in the early years of the study, while some species shifted towards the lower part of the axis in the latter years (Figure 2.3a-c).

Except for a few, most of the species in the no burn plots (1 CON and 2 CON) formed a distinct cluster towards the positive side of the axes, and were generally closer together, indicating that their species composition was less variable than those of the burnt plots. On the other hand, the burnt plots formed less distinct clusters, with more scattered plots, suggesting that burning may have promoted a more variable species composition. The triennial and quadrennial burns resulted in the most scattered plots, followed by the annual and biennial burns, while the six-year burn was the least scattered of the burnt plots, having ordination plots that were almost indistinct from the control plots (Figure 2.2).

The trajectories for each treatment (with replicates kept separate) are presented in Figures 2.3a, b and c respectively. When the trial commenced in 1980, species composition in all the 12 treatment plots was similar, but the variability increased over time, especially in the ten burnt plots. Some of the years that were either too

close or overlapping have been omitted from the graphs to reduce overcrowding. There appeared to have been a sharp compositional shift between 1982 and 1985 across all the treatment plots, and after 1988 the variation gradually stabilized (Figures 2.3 a, b and c). The triennial and quadrennial burns produced the longest ordination distances between 1982 and 1983 (Figure 2.3b), followed by the no burn and sexennial burns (Figure 2.3c), while the annual and biennial burns had the shortest distance (Figure 2.3a). Furthermore, some variation was also apparent between the two replications of each treatment, with the highest noticeable variation in the triennial and quadrennial burns (Figure 2.3b).

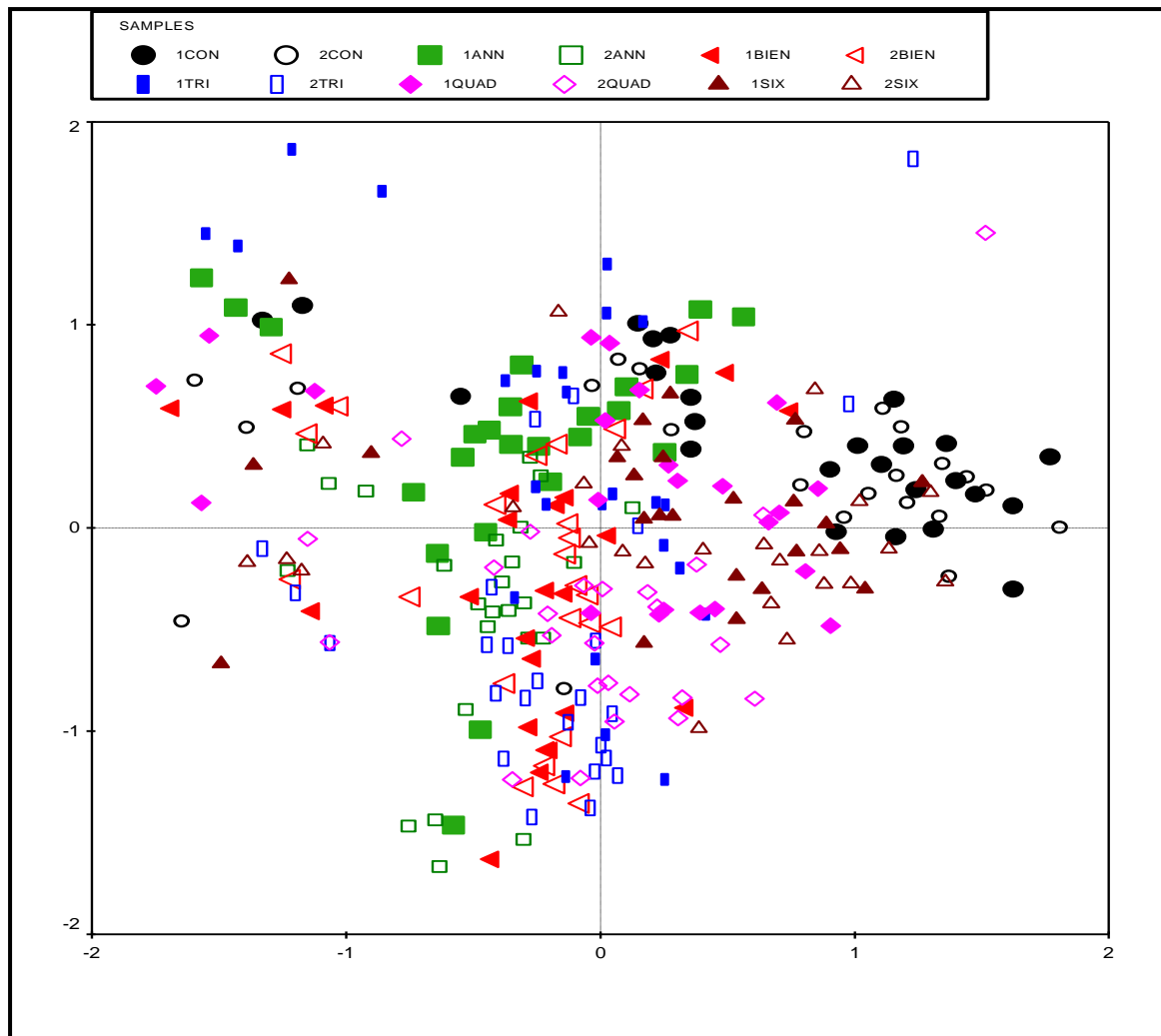


Figure 2. 2 NMS sample ordination plots of species composition in a long-term fire trial at Fort Hare research farm between 1980 and 2008.

KEY: 1CON= No burn 1, 2CON= No burn 2, 1ANN =Annual 1; 2ANN= Annual 2, 1BIEN= 1Biennial, 2BIEN = 2Biennial, 1TRI = 1Triennial, 2TRI = 2Triennial, 1QUAD = 1Quadrennial, 2QUAD= 2Quadrennial, 1SIX = 1Sexennial, 2Six = 2 Sexennial.

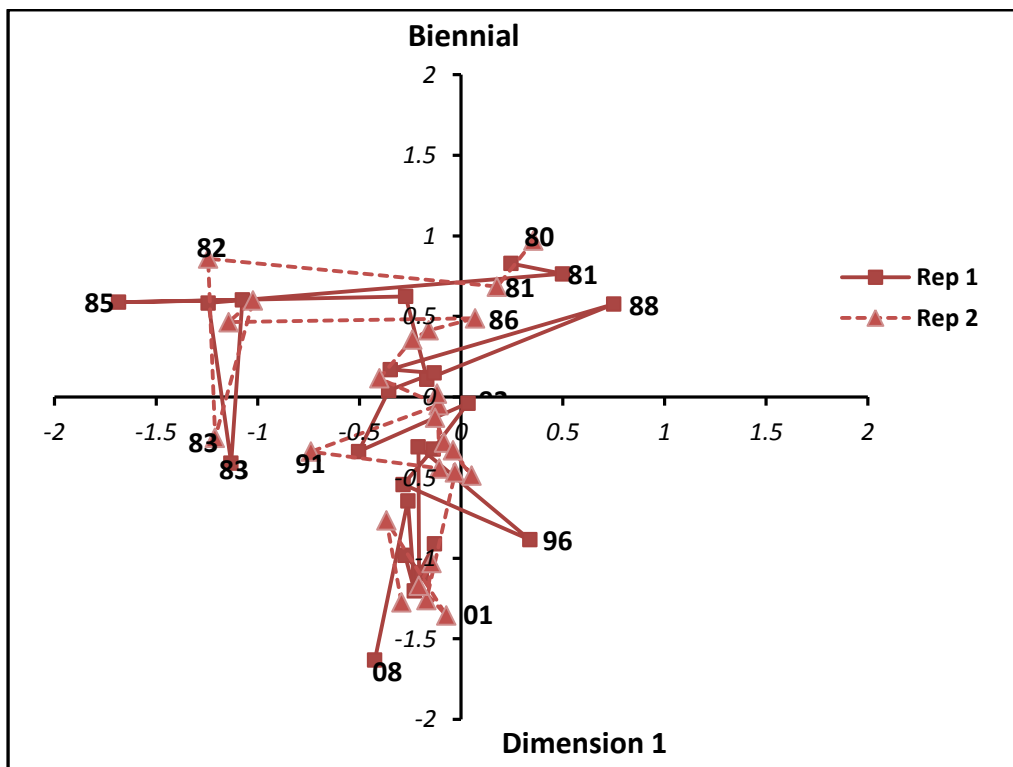
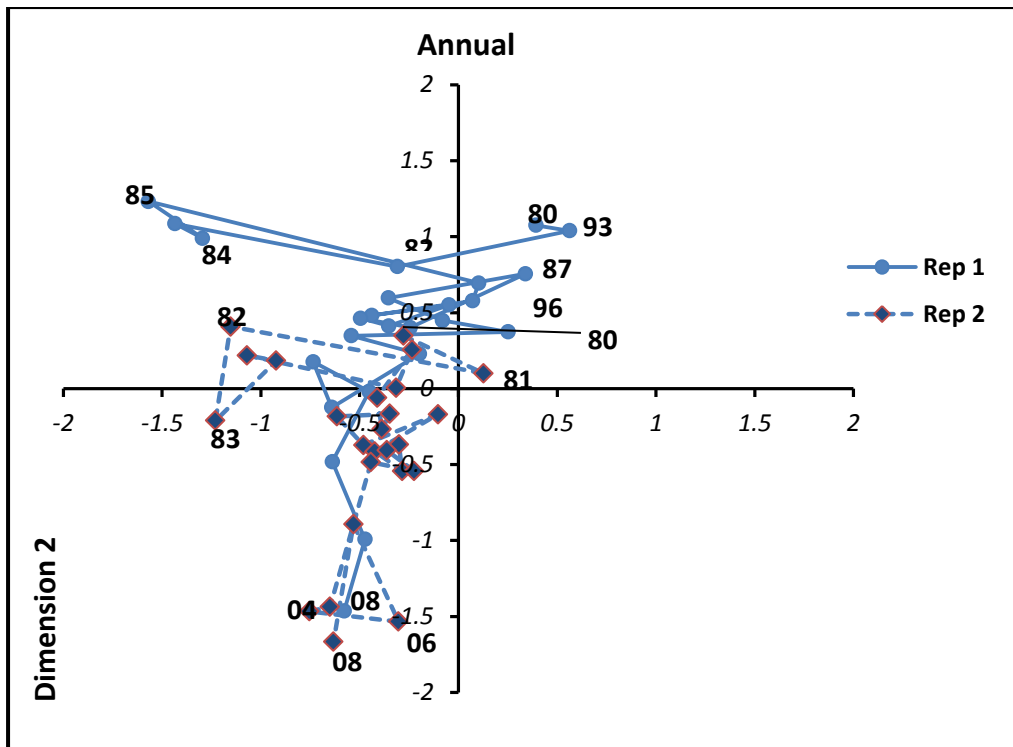


Figure 2. 3a NMS trajectories of species composition for the annual and biennial burns of the long-term fire trial.

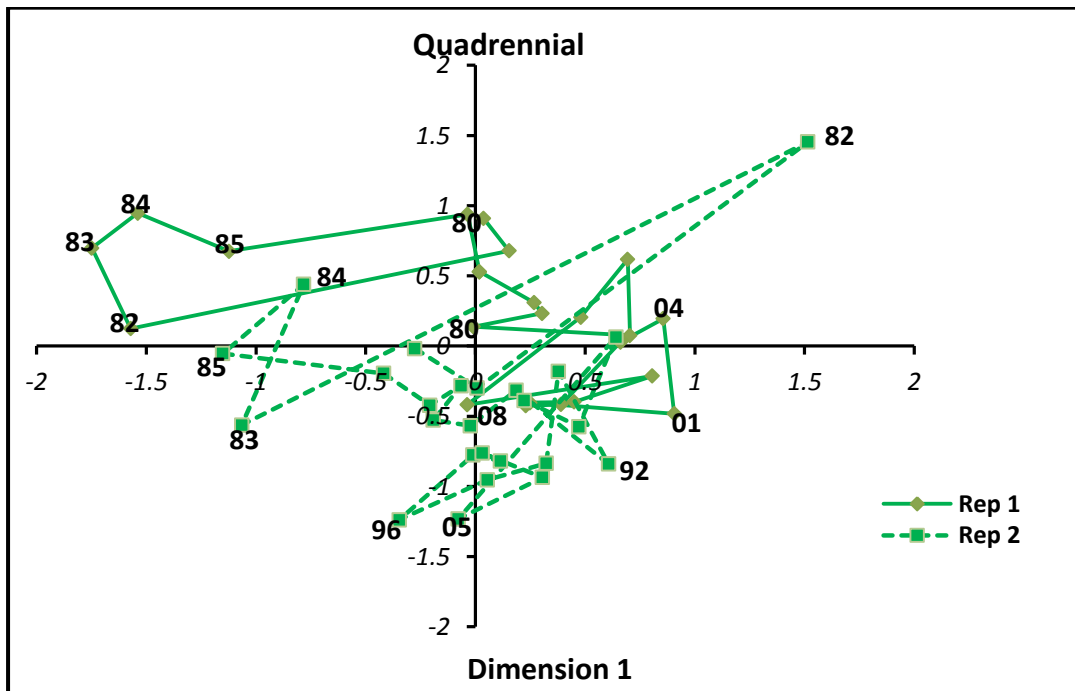
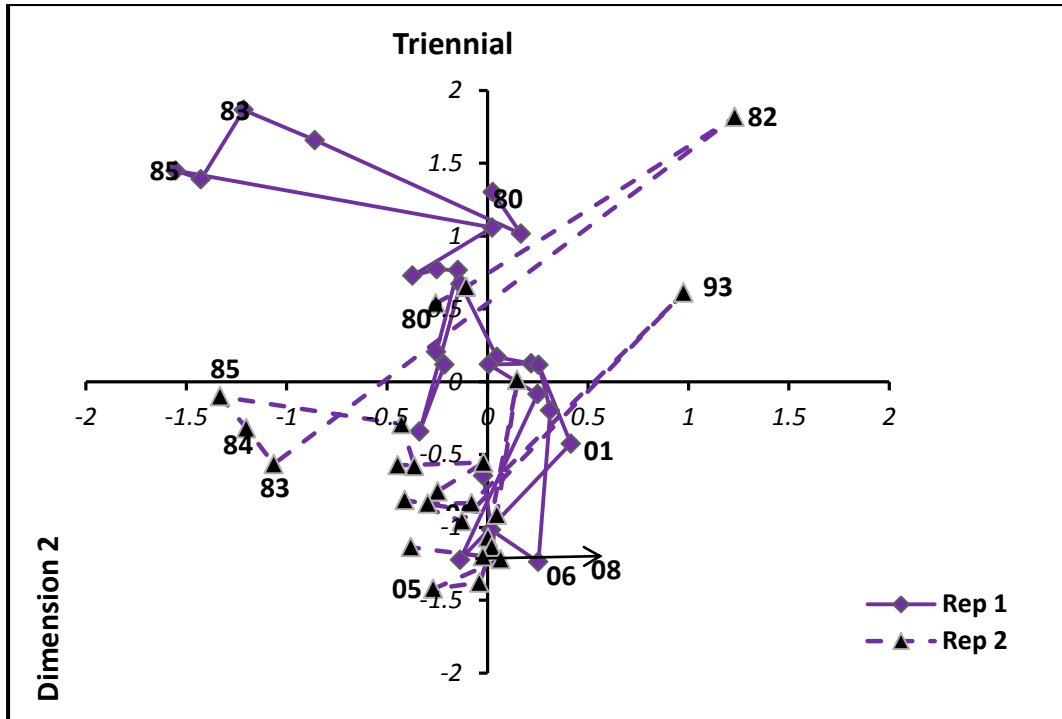


Figure 2.3b NMS trajectories of species composition for the triennial and quadrennial burns of the of the long-term fire trial

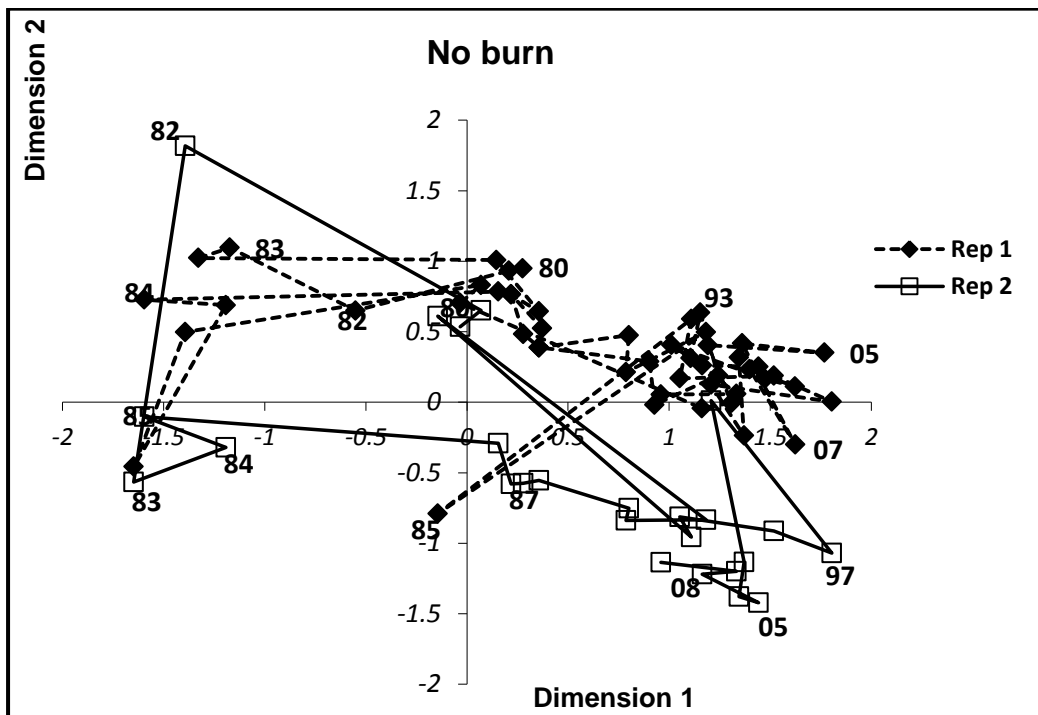
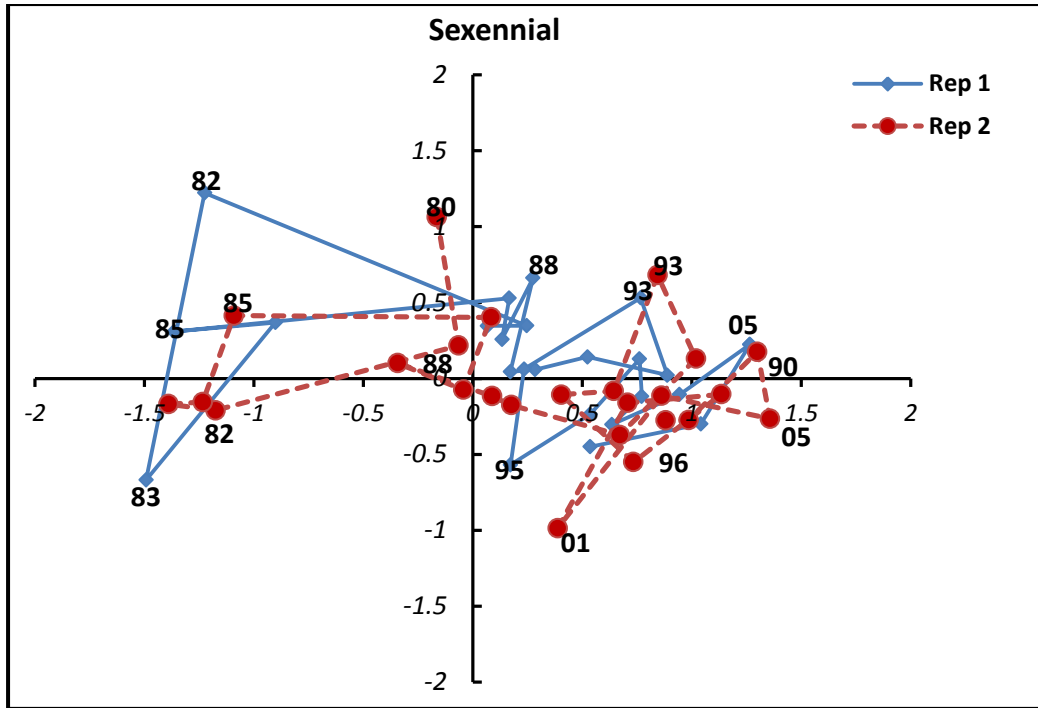


Figure 2.3c NMS trajectories of species composition for the sexennial and no burn treatments of the of the long-term fire trial

2.3.2 Species trends in the Nonmetric Multidimensional Scaling

A total of eighteen grass species and some unidentified forb and karroid species were recorded and included in the analyses of this study. Figure 2.4 is the NMS ordination species which were abundant in most of the treatment plots. The results indicate that herbaceous species abundances and distribution were influenced by fire treatments, and the variation increased with time, whereby species spread along gradients of increasing/decreasing fire frequency over time. *Cymbopogon plurinodis* (though the abundance was generally low), *Melica decumbens*, *Sporobolus fimbriatus*, Karroo and Forb species were mostly found in the upper right quarter where treatment plots were mainly the sexennial and quadrennial and no burn controls (Figure 2.4, 2.5b,c). Actually, *M. decumbens* was completely eliminated from the annual, biennial burns, and was almost absent in the triennial burns as well. Conversely, *Themeda triandra* was most dominant in the annual and biennial plots and became less abundant as fire frequency decreased (Figure 2.5a). Several species such as *Digitaria eriantha*, *Eragrostis species*, *Panicum stapfianum* and, *Sporobolus africanus* were also abundant in the top left quarter where frequent burns were applied, which also occurred during the first five years of the experiment (Figure 2.3a-c, 2.4).

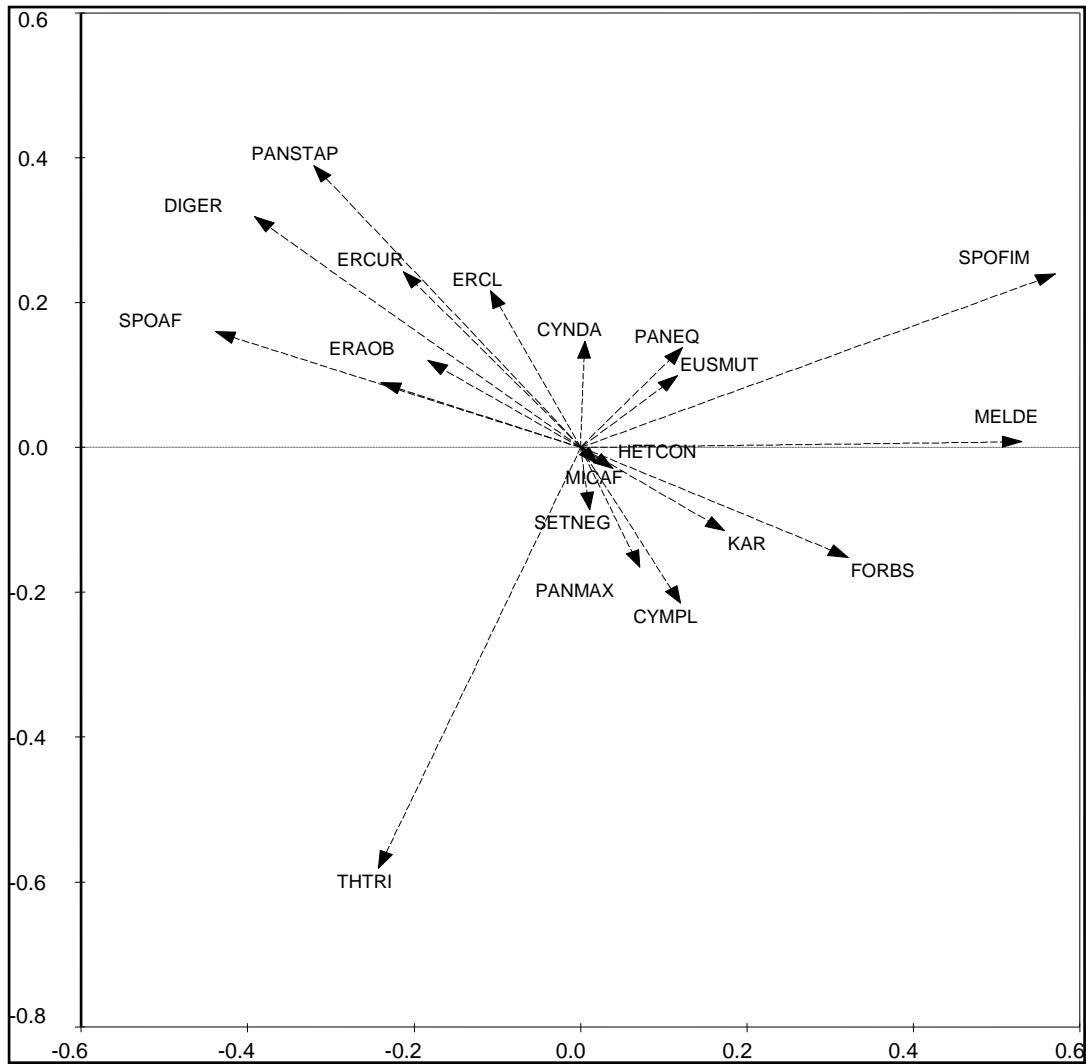


Figure 2.4 NMS ordination of species composition in a long-term fire trial at FortH

Hare research farm

KEY: CYNDA= *Cynodon dactylon*, CYMPL = *Cymbopogon plurinodis*, DIGER = *Digitaria eriantha*, ERCUR= *Eragrostis curvula*, ERCL = *Eragrostis chloromelas*, ERAOB = *Eragrostis obtuse*, EUSMUT = *Eustachys mutica* (changed to *Eustachys paspaloides*), HETCON = *Heteropogon contortus*, KAR= All Karroo species, MELDE= *Melica decumbens*, MICAF = *Microchloa caffra*; PANEQ = *Panicum aequinerve*, PANMAX = *Panicum maximum*, PANSTAP = *Panicum stapfianum*, SPOAF = *Sporobolus africanus*, SPOFI= *Sporobolus fimbriatus*, THTRI = *Themeda triandra*.

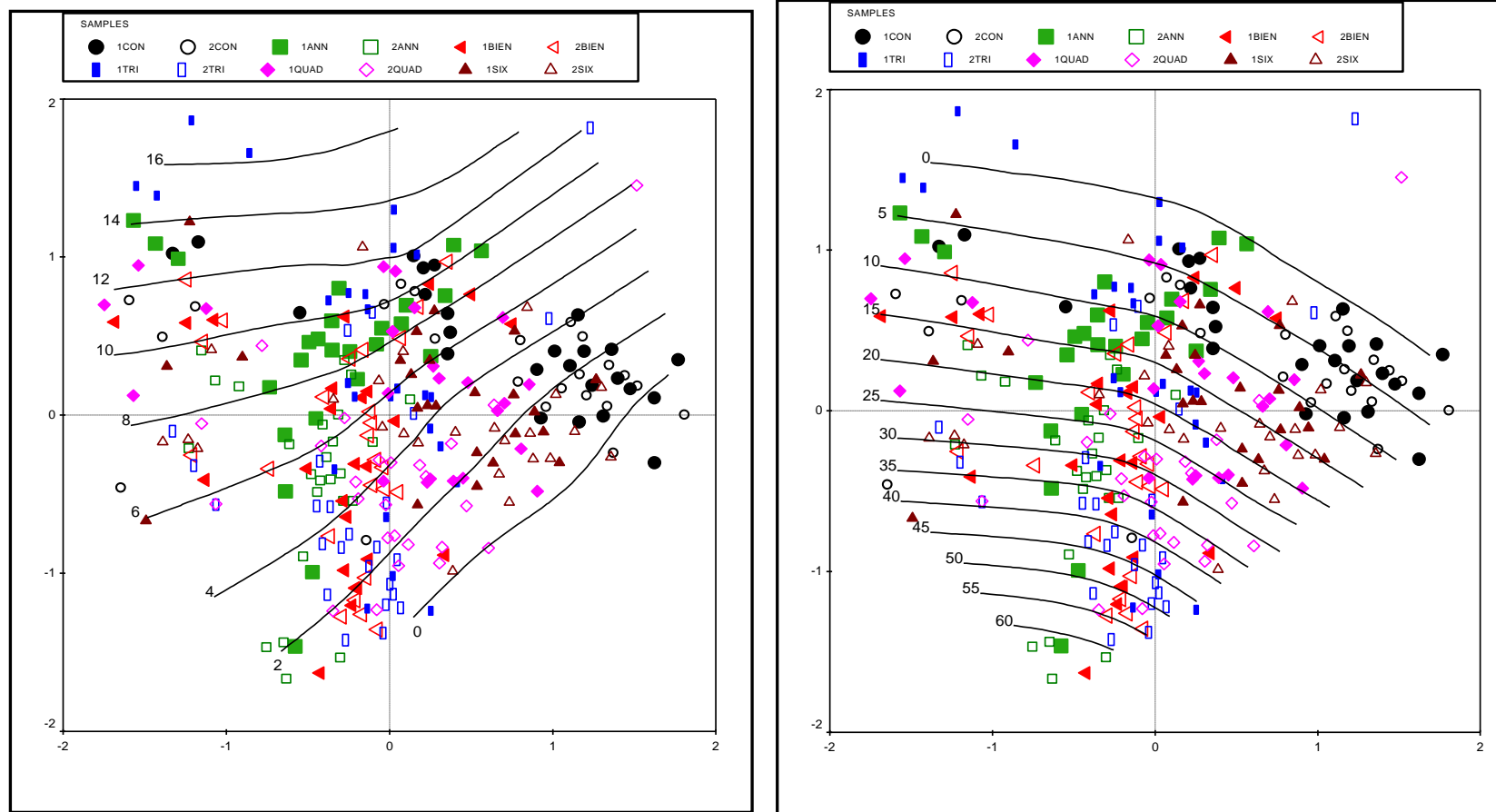


Figure 2.5a NMS ordinations for mean abundances for *Panicum stapfianum* (left) and *Themeda triandra* (right) across the burning treatments

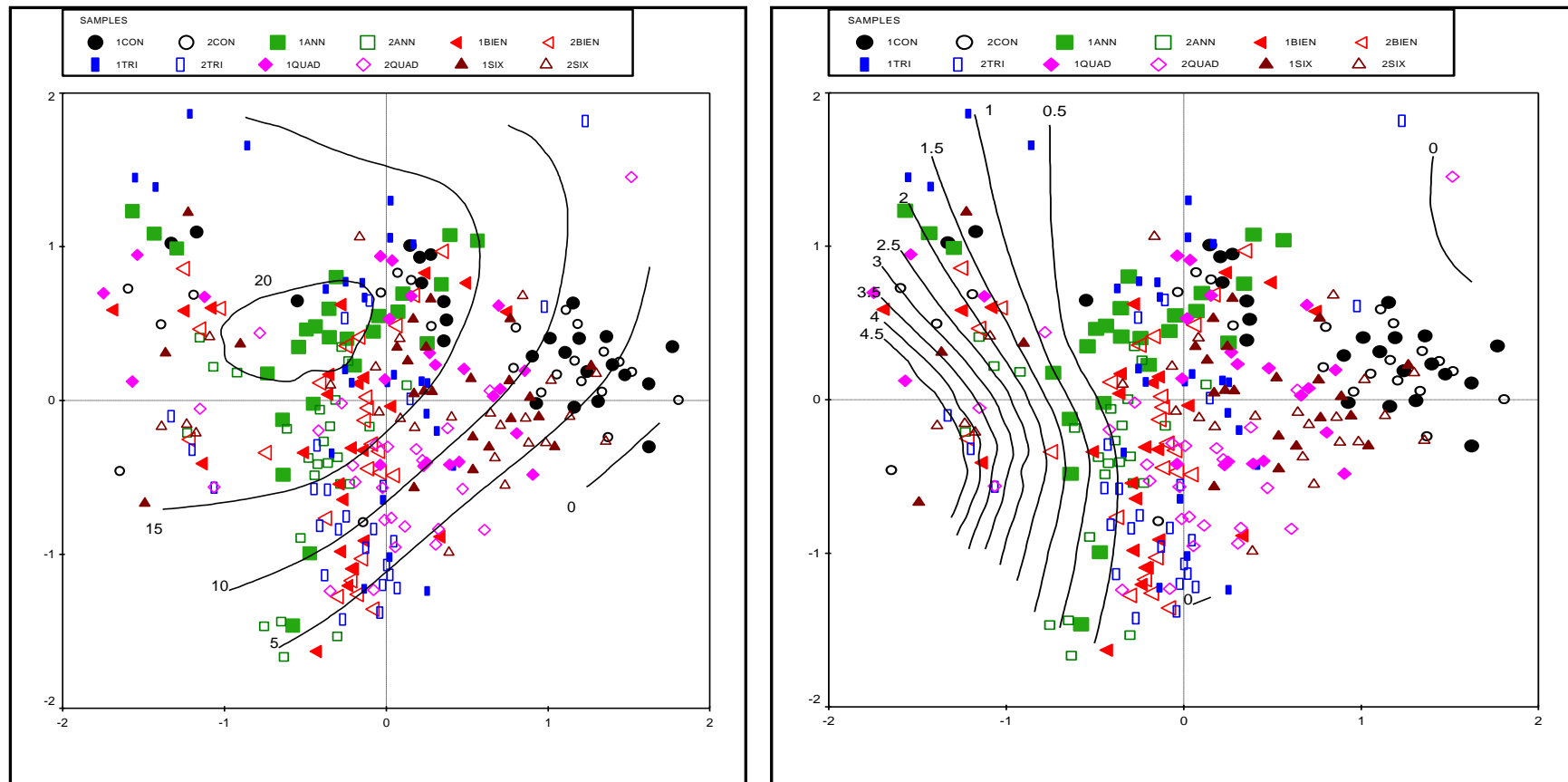


Figure 2.5b NMS ordinations for mean abundances for *Digitalia eriantha* (left) and *Sporobolus africanus* (right) across the burning treatments

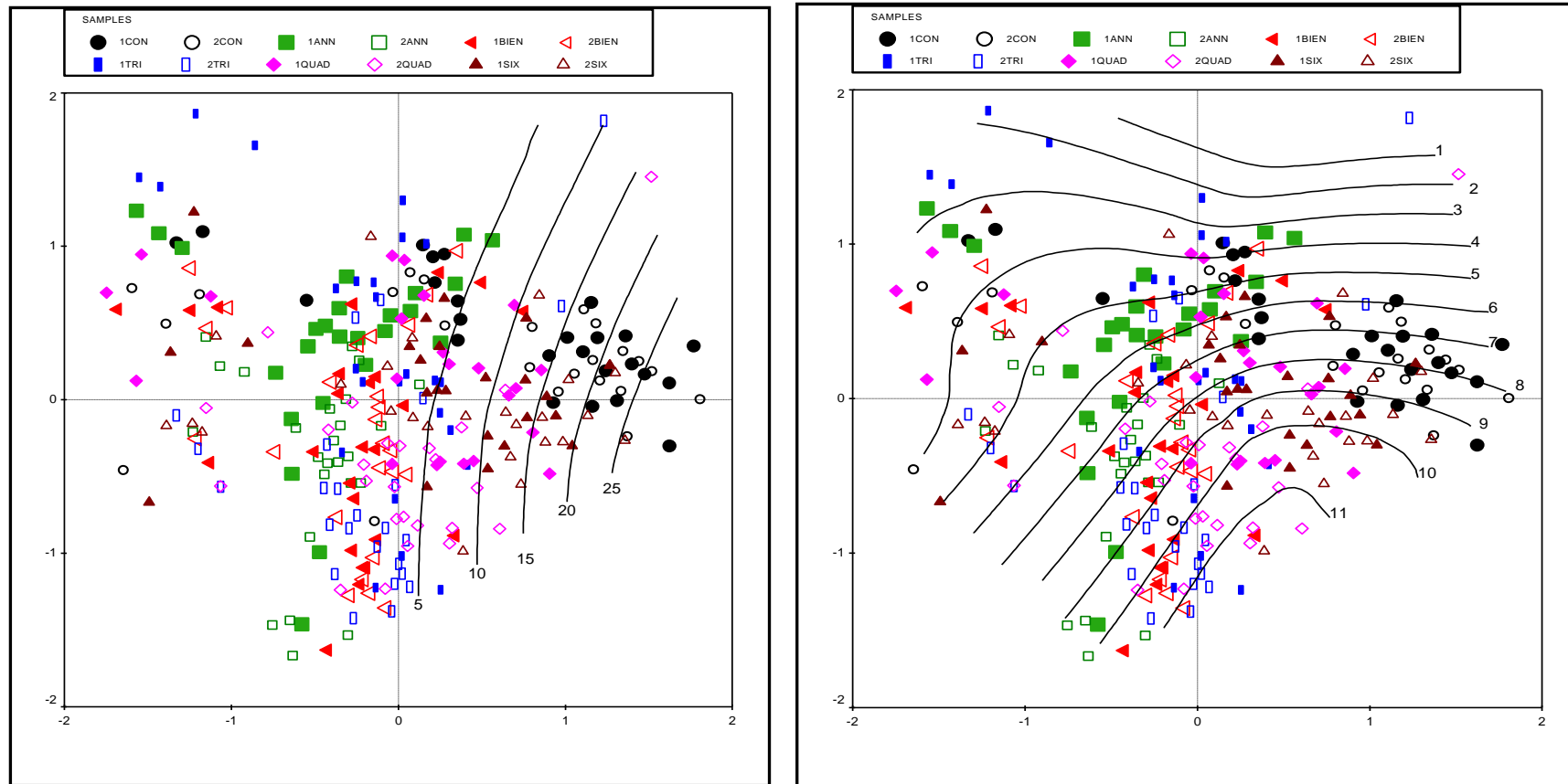


Figure 2.5c NMS ordinations for mean abundances for *Melica decumbens* (left) and *Cymbopogon plurinodis* (right) across the burning treatments.

2.3.3 The Bray-Curtis dissimilarity analysis

The Bray-Curtis dissimilarity test indicated varying degrees of dissimilarity between burnt and unburnt plots, as well as between the no burn plots themselves (Table 2.2). The mean dissimilarities between unburnt 1 and burnt plots were 25.7 % in 1980 and 62 % in 2008. Moreover, the two unburnt plots were 20.5 % dissimilar in 1980 and 29 % in 2008. The mean dissimilarity coefficients suggest that species composition in 1980 was more comparable amongst the treatments, but with time those of frequently burnt plots (annual and biennial) varied more in composition from the unburnt plots than the less frequently burnt plots (Table 2.2). The percentage dissimilarities for the annual and biennial plots (77.1 and 70.5 % respectively) were higher than those of the triennial, quadrennial and sexennial plots respectively (Table 2.2). In 2008, the composition for the no burn (1) was 59 % different from the way it was in 1980.

Table 2. 2 Mean Bray-Curtis % Dissimilarity in species composition between no burn (1) and treatment plots in 1980 and 2008. ($P \leq 0.05$; LSD = 13.7).

Treatment	Bray-Curtis % Dissimilarity	
	1980	2008
Annual	23.9	77.1
Biennial	22.5	70.5
Triennial	24.9	57.5
Quadrennial	30.2	51.1
Sexennial	27.1	53.7
No burn (2)	20.5	59.0

2.4 Discussion

Unlike other processes that threaten biodiversity, fire is an environmental phenomenon that can threaten or benefit biodiversity depending on fire regimes (Trollope 1983). In this trial, the NMS ordinations indicate that burning treatments have altered species composition to a higher degree than unburnt sites, whereby plots burnt exhibited stronger compositional variation than no burn controls (Figure 2.2; 2.3a-c). In a similar trial at Ukulinga farm, Fynn (et al. 2004) reported that long-term protection from dormant-season burning resulted in a 55 % decrease in species richness relative to burnt sites. However, in this study more frequent burns (annual and biennial burns) appeared to be a regime that had negative effects on species composition since it reduced compositional variation by reducing the abundances of less fire-tolerant species (Figure 2.4), and consequently eliminating species such as *Melica decumbens* (Figure 2.5c) that are highly sensitive to fire. Gary and Morrison (1995) also established that short-fire intervals are associated with a reduction in the number of species present in the community.

In this study, the triennial and quadrennial burns exhibited the most diverse composition (Figure 2.2, 2.3b), and these results appear to support the theory pointed out by Uys (et al. 2004), which states that species richness should be highest at intermediate levels of disturbance. Morrison (et al. 1995) also highlighted that increasing time since fire is associated with a decline in the evenness of fire-tolerant herbaceous species, giving an opportunity for fire-sensitive species to also establish. Forbs and karroid species also decreased with fire frequency. This could be attributed to the fact that unlike grasses which have basal meristems, most forbs have aerial meristematic regions, which make them more vulnerable to defoliation by frequent burning.

As already highlighted, savannas historically experience wildfires and the species respond differently to fire regimes depending on their life history strategies. In this experiment, the species' responses to long-term burning frequency were grouped into three main categories: The first category comprised the species that increased in abundance with burning frequency such as *Themeda triandra*, *Digitaria eriantha*, *Panicum stapfianum* and *Eragrostis* species. The second comprised those that

decreased with burning frequency such as *Melica decumbens*, *Cymbopogon plurinodis*, forbs and karroo, and the third group of species did not appear to be significantly affected by burning frequency. Species belonging to the same genus also responded in exact opposites to burning frequency: e.g *Sporobolus fimbriatus* was most abundant in the control burnt plots, while *Sporobolus africanus* was mostly in the annual and biennial plots (Figures 2.4; 2.5b). The responses of these species demonstrate or support that some species are fire-tolerant and hence thrive in frequently burnt areas, while others are fire intolerant and thrive in less frequently burnt areas and in the absence of fire.

The Bray-Curtis dissimilarity comparisons (Table 2.2) showed that species composition in the experimental site was more similar between experimental plots in 1980 prior to commencement of the trial. After 28 years of burning treatments, the annual and biennial burns were notably dissimilar to the no burn treatments, while the dissimilarities with the triennial, quadrennial and sexennial burns were comparably lower than those of frequent burns. The increase in compositional variation over time results from the reduction or elimination of non fire-tolerant species such as *Melica decumbens*, which disappeared from the frequently burnt plots dominated by *Themeda triandra* and few other species. In other studies conducted the False Thornveld of the Eastern Cape, frequent burning enhanced the abundance of *T. triandra*, but had a negative effect on the abundance of *Cymbopogon plurinodis* (Frost and Robertson 1985; Trollope 1999; Uys et al. 2004). *T. triandra* also increased in frequently burned areas in Australia (Morgan and Lunt 1999; Lunt and Morgan 1999). These reports show that a massive compositional shift may occur where burning is applied at short intervals. The fact that composition in the second no burn replicate was as different from the first replicate as less frequently burnt plots illustrates the dynamic nature of ecological systems, which is driven by an array of biotic and abiotic environmental factors that inevitably result in compositional change.

2.5 Conclusions

From this study, it is apparent that fire is an agent of change that performs a variety of functions and produces a range of effects. The study has demonstrated the theory of fire-tolerance and fire-intolerance among herbaceous species. Frequent fire and its absence had positive effects from a range management standpoint, but negative effects from a conservation standpoint, in that it reduced the abundances of, or even eliminated fire-intolerant species, reducing species richness and diversity. Frequent burning resulted in a less variable species composition, and the dominance of fire-tolerant herbaceous species, primarily *Themeda triandra*, which is highly acceptable to livestock, but eliminated fire-intolerant species. The absence of fire promoted the abundance of fire-intolerant species such as *Melica decumbens*, and though there was higher compositional variation than in frequent burns, these species are not highly acceptable to livestock. Other species such as *Panicum maximum* and *Sporobolus fimbriatus* exhibited little response i.e. neither increased nor decreased with burning frequency. It was hypothesized that fire would influence species composition by favouring fire-tolerant species under high burning frequencies and fire-intolerant species at lower frequencies according to individual plant history strategies, promoting maximum overlap of species at intermediate frequencies. The results of the study have not disproved it, therefore the hypothesis is not rejected.

The triennial and quadrennial burns exhibited the most diverse herbaceous species composition after 28-years period of burning treatment, with the abundance of both fire tolerant and fire intolerant species. These two burning frequencies appear to be suitable when using fire as a management tool primarily for conservation purposes in the False Thornveld of the Eastern Cape. These could maintain biological diversity by enhancing the productivity of fire-dependent decreaser species such as *Themeda triandra*, but will also not eliminate fire-intolerant species which are part of the ecological system. However, this conclusion was based on the results obtained in the absence of grazing, and may not be applicable to most of the rangelands in this area where grazing by domestic livestock is generally practiced. In many cases, burning may not be necessary, but if deemed necessary, intervals longer than 3-4 years would be recommended. The study has also demonstrated the dynamic nature of natural

systems, and as illustrated by the species ordination, the magnitude and direction of compositional change is closely related to the responses of individual species to a specific environmental factor. As fire is an important driver of many ecological systems, long-term trials such as this provide better understanding of the role of fire in their dynamics. However, one should be cautious because, as highlighted by Trollope (1983), factors such as overgrazing, drought and frost complicate the interpretation of results ascribed to the responses of the vegetation to a particular burning treatment.

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CHAPTER 3 LONG-TERM EFFECTS OF BURNING FREQUENCY ON LIGHT INTERCEPTION AND BIOMASS PRODUCTION IN A SOUTH AFRICAN SAVANNA

Abstract

A study was conducted to investigate the long term effect of fire frequency on light interception and biomass production in the False Thornveld of the Eastern Cape (32° 47' S; 27° 01' E). The study was carried out on a long term trial set up in 1980 at the University of Fort Hare research farm, and treatments comprise annual, biennial, triennial, quadrennial, sexennial burns and a no burn control. Each treatment is replicated twice in a Completely Randomized Design. Photosynthetically Active Radiation (PAR) and Leaf Area Index (LAI) were measured on grass leaf canopies using a Decagon AccuPAR LP-80 Ceptometer, on cloudless days April and December 2006 between 11h45 and 13h30. Aboveground biomass of herbaceous vegetation was determined by harvesting all herbaceous material within randomly placed 1 m² quadrants at ground level. Treatment effects were tested using Analysis of Variance, and Least Significant Difference tests were used to separate treatment means. Regression analyses were used to test relationships between light interception and biomass production.

Treatments significantly affected the percentage of Intercepted Photosynthetically Active Radiation (%IPAR), Leaf Area Index (LAI) and aboveground biomass production. Frequent fire and its absence resulted in the lowest light interception and biomass production. The three-year burn resulted in the highest light interception, LAI and aboveground biomass production (g/ m²/), while annual, biennial and no burn treatments resulted in the lowest biomass production. The %IPAR and LAI for the annual and biennial burns were significantly lower than that of the triennial burn, while the quadrennial, sexennial and no burn treatments did not significantly differ from the triennial burn. Biomass productions for the annual, biennial and no burn treatments were also significantly lower than those of the triennial burn. There was a significant positive polynomial correlation between %IPAR and aboveground biomass ($r^2 = 0.58$; $P \leq 0.05$). Based on these results, in the absence of grazing,

burning every 3 to 6 years is recommended for maximising vegetation productivity because rejuvenation by fire maintains a higher level of productivity in semiarid savannas by improving light interception.

Keywords: Fire frequency, herbaceous species, light interception, Photosynthetically Active Radiation, Leaf Area Index, aboveground biomass production.

3.1 Introduction

3.1.1 Solar radiation and energy flow in ecological systems

A functional ecological system depends on the flow of energy (Richmond et al. 2007), which in turn is primarily determined by light that is available to plants. In thermodynamic terms, ecosystems are machines supplied with energy from an external source, the sun (Monteith 1972). Through photosynthesis, this thermonuclear energy is absorbed by chlorophylls and other pigments, and converted to chemical energy, the usable form for higher organisms (Rascher and Nedbal 2006). The capacity of ecological systems to produce biomass may appear limitless given the large, continuous supply of solar radiation. However, primary productivity (i.e. plant growth/area/time) is quite low in some grasslands ($< 2000\text{kg/ha/year}$) (Sala et al. 1988). Low productivity in ecological systems is generally a result of two main ecological constraints:

- ❖ The first constraint is the quality of solar radiation available at the earth's surface (Briske and Heitschmidt 1991).
 - Only about 45 % of the solar energy is within the appropriate region of the spectrum (i.e. wavelengths between 370 nm and 760 nm) that is effective in photosynthesis.
 - The remaining 55 % is long wave radiation absorbed as heat energy by the atmosphere, soil and vegetation, is unavailable for conversion into chemical energy through photosynthesis (Briske and Heitschmidt 1991; Wright 1990).
 - The 45% of solar radiation available in the absorbing spectra of plant leaves also fluctuates spatially and temporally due to changes in solar position, cloud movement and vegetation structure. Moreover, the efficiency of conversion of insolation into stored carbohydrates (chemical energy) is limited by many leaf-level morphological, physiological and metabolic (e.g. photorespiration) factors, resulting in a typical conversion efficiency of 3–6%.

- ❖ The second constraint limiting primary productivity is the occurrence of abiotic and biotic conditions which prevent solar energy capture from being maximized.
 - Water, temperature and nutrient limitations often prevent a sufficient leaf canopy from developing to intercept available solar energy (Begon et al. 1986; Briske and Heitschmidt 1991).
 - In recent years, humans have also diverted or prevented about 20% to 30% of solar energy from flowing through natural ecosystems by maintaining croplands (15%), urban areas (1.8%), and by grazing livestock (2.3%). Habitat degradation, mainly in the form of desertification, has also caused a 4 % reduction (Wright 1990).

Two thermodynamic laws govern energy flow in biological or ecological systems: The first law says that energy is neither created nor destroyed, but can be converted from one form to another. In other words, when the input of energy to an ecosystem is equal to its output energy, this results in the state of equilibrium, and in nature this is rarely the case. The second establishes that energy conversion processes are not 100 % efficient. It implies that the production of “useful” energy in any process must be accompanied by a simultaneous energy “waste.” These two laws highlight that a large proportion of the chemical energy made through photosynthesis and transferred between trophic levels, is converted to heat which is of little value to the biota (Monteith 1972). The energy “loss” between feeding levels results from an inefficient transfer of organic matter, and also due to the energy required or used for the internal maintenance of organisms.

Ecological systems are highly dynamic, and to enhance the efficiency of energy flow and increase primary and secondary production, the roles of key environmental factors on the capture of solar radiation should be clearly understood.

3.1.2 Photosynthetically Active Radiation and Leaf Area Index

The fraction of Photosynthetically Active Radiation (fPAR) absorbed by vegetation and Leaf Area Index LAI) are essential measurements for characterizing vegetation

canopy functioning and energy absorption capacity (Mynenni et al. 2002). PAR and LAI are key biophysical parameters used in most ecosystem productivity models of climate, hydrology, biogeochemistry and ecology (Sellers et al. 1997; Yang et al. 2007). The response of plant canopies to radiation is a function of the intensity of radiation in various spectral regions, and the absorbing and transmitting properties of the vegetation (Law and Waring 1994). The spectral properties of leaves and multiple reflections between them make vegetative canopies highly absorbent in the visible wavelength interval due to photosynthetic pigments, and moderately reflective in the near-infrared region due to inter and intra-leaf scattering (Sellers et al. 1997; Woodward 1983). Chlorophyll absorbs in the three major wavebands, blue (400-500 nm), red (550-700 nm) and far-red (550-800 nm) so that the light reflected and transmitted by leaves is predominantly green (Law and Waring 1994; Monteith 1972).

PAR measurements indicate how much useful light is available to plants for photosynthesis, and are hence used in assessing the health and status of a plant canopy. The percentage or fraction of intercepted PAR (%IPAR or fIPAR) measures the proportion of available radiation in the photosynthetically active wavelengths that a canopy actually absorbs, and their values range between 0.0 and 1.0 (Knyazikhin et al. 1998b). The fPAR is represented by the following formula obtained from Serrano et al. 2000):

$$(1 - I/I_0)$$

Where: I is the irradiance below plant canopy

I_0 is irradiance above the canopy.

Fractional intercepted PAR differs from the fraction of absorbed PAR (fAPAR) due to PAR being reflected from the soil or litter surface and from the canopy itself (Serrano et al. 2000).

Leaf area is the exchange surface between the photosynthetically active component of vegetation and the atmosphere and controls the light, thermal and hydric conditions of within a plant canopy (Arias et al. 2007). Leaf Area Index is defined as one-sided green leaf area per unit ground area in broadleaf canopies and as the projected needle leaf area in coniferous canopies (Mynenni et al. 2002). This parameter directly

determines the energy balance, net primary production and evapo-transpiration (Wang et al. 2007). Studies conducted to investigate the relationship between the fractions of PAR intercepted and LAI have indicated an asymptote at LAI of between 4 and 6 (Law and Wring, 1994). For example, Asrar (et al. 1984) found that PAR absorption by winter wheat increased rapidly with an increase in LAI and levelled off above 6.0. Ground measurements of PAR transmittance have been used to derive LAI values based on the Beer-Lambert law of exponential light extinction in plant canopies:

$$I/I_0 = \exp(-K*LAI)$$

where : I is irradiance below plant canopy,

I_0 is irradiance above the canopy,

LAI is the projected leaf area index.

K is the Leaf Extinction coefficient for PAR (Jarvis and Leverenz 1983).

Both LAI and fIPAR have been extensively used as satellite derived parameters for calculation of surface photosynthesis, evapo-transpiration and net primary production in many studies worldwide (e.g. Sellers et al. 1997; Knyazikhin et al. 1998b; Serrano et al. 2000; Myenni et al. 2002), while fIPAR is also an important parameter in modelling ecological function, crop growth, atmosphere and biogeochemical functions (Yang et al. 2007). In this study, the effects of long term fire frequency on these two parameters were investigated, as well as their effects on primary productivity as influenced by fire frequency.

3.1.3 Solar radiation and biomass production

Plant biomass is known to be one of the most promising renewable energy sources that can be used for production of bio-fuels since it is an abundant resource, has low CO₂ emissions and has low input cost (Zhao et al. 2009). Moreover, plant biomass for biofuel production can contribute to a stabilization of farmers' incomes, and can maintain and improve ecological and social sustainability (Parrika 2004; Xiong et al. 2008). The abundant radiation in the tropics and sub-tropics provides a great

opportunity to increase primary production to meet the ever-increasing demands for the world's rapidly increasing population. As stated by Awal (et al. 2006), production could be achieved through efficient harvesting and use of solar radiation in these areas where there is high demand for food, fuel and oil. However, primary production is not always limited by the quality or quantity of incident radiation. It is greatly influenced by prevailing biotic and abiotic environmental factors, and a deeper understanding of how these factors affect community productivity in each ecological zone will assist in developing management plans for enhanced production and sustainability.

Tropical and subtropical grasslands and savannas are characterized by distinct dry and wet seasons that are coupled with high temperatures and highly variable rainfall (Chirara et al. 2001). To survive or be productive, tropical and subtropical plants have to be adapted to highly temporally variable environmental conditions. Plant metabolism is generally based on the photosynthetic reaction, in which shortwave radiation energy is used to combine water and atmospheric CO₂ into sugars and other organic compounds. Primary production is therefore directly linked to the percentage of incident photosynthetically active radiation intercepted by vegetation, and potentially used for photosynthesis (Monteith 1972). A number of models have been developed to show how the amount of light intercepted by vegetation is a key determinant of production. Studies have shown that net primary production (NPP) is linearly related to annual IPAR (megajoules per square meter per year) under ideal conditions. Monteith (1972) developed an empirical formula as follows:

$$\text{NPP} = \text{IPAR} * \epsilon,$$

Where:

ϵ is energy conversion efficiency of 1-5 g of dry matter produced per mega joule of energy absorbed.

The measurement of PAR and determination of its role on community dynamics is being enhanced by technological advancement such as PAR ceptometers, which allows one to quantitatively determine the amount of PAR on a particular system below and above plant canopy. The AccuPAR ceptometer gives both values of PAR above and below plant canopies, and LAI is automatically calculated by the same instrument after taking PAR measurements above and below plant canopies. Ground measurements of photosynthetically active radiation (PAR) transmittance have been

used to derive LAI values based on the Beer-Lambert law for exponential light extinction in plant canopies (Jarvis and Leverenz 1983).

Accordingly: $I/I_0 = \exp(-K \times LAI)$

Where:

I is the irradiance at the depth z from the top of the canopy,

I_0 is irradiance at the top of the canopy,

LAI is the projected Leaf Area Index, and

K the leaf extinction coefficient for PAR.

LAI is arguably a powerful diagnostic of plant productivity, but remains difficult to quantify accurately due to large spatial and temporal variability in vegetation (van Wijk and Williams 2005). A number of factors such as climate and disturbance can also influence light availability or penetration to individuals and the system as a whole, of which disturbance in the form of fire and herbivory are commonplace in many regions across the globe. These two forms of disturbance are natural factors in grasslands and savannas, and an investigation of their role in the interception of solar energy and community production is warranted.

3.1.4 The role of fire on light interception and biomass production

The effect of fire on vegetation is determined by fire regimes, i.e. different aspects of burning comprising season, frequency, intensity and type of fire (Trollope 1983; Bond and van Wilgen 1996). Each of these regimes plays its role when fire occurs. Fire frequency is the number of fires experienced by a particular community within a given time period (Morrison et al. 1995). In the arid savanna the frequency of fire is generally lower than in the moist savannas because the rainfall is both less and highly erratic, and the grass sward remains acceptable to grazing animals even when matured. Fire also affects the environment indirectly by removing or reducing plant and litter cover, thereby modifying both the post-fire microclimate and the activity of soil biota (Bond and van Wilgen 1996). Fire also results in a younger re-growing leaf canopy with different photosynthetic efficiency than a mature sward. In this semi-arid savanna referred to as the 'False Thornveld of the Eastern Cape, fire is commonly used to remove top hamper or moribund grass material; to control undesirable plants,

especially woody species encroachment; to prepare the land for cultivation; to kill insects and also to facilitate hunting (Trollope 1989; Jacobs and Schloeder 2002). A decision to burn or not depends on rangeland condition, and the key indicators of ecological status that are required for making a decision to burn are species composition, basal cover and fuel load. Burning is usually applied during the dormant season (winter to early spring) because least damage is done to grasses when they are not actively growing (Trollope, 1989). When burning during winter and early spring, grasses recover quickly and soil erosion is minimal and this results in an increase in forage production in the future, while burning rangeland in late spring (October) can delay grass recovery until November. (Everson et al. 1988). The most common types of fire are surface head fires with intensities ranging from a cool fire (≤ 1000 kJ/s/m) to a high intensity fire (≥ 2000 kJ/s/m) depending on the amount and type of fuel load as well as time at which fire occurs (i.e. whether winter or spring).

Many of the studies investigating the role of fire on light interception and/or primary production were conducted on forest ecosystems (e.g. Viro 1974; Engelmark 1993; Skre et al. 1998; Ansley et al. 2002; Arias et al. 2007; Wang et al. 2007), leaving opportunity to explore other systems where fire is a driver. Grasslands and savannas are prone to wildfires due to litter accumulation during winter in more mesic areas and those that are not heavily grazed. Fire is often used in these areas to increase grassland dominance and suppress woody plant encroachment because it is often considered the most cost-effective and ecologically sound treatment as compared to other options (Wright and Bailey 1982; Scholes and Archer 1997). However, its role in light interception and primary productivity of herbaceous vegetation is not well documented. In light of global economic challenges and the increase in food demand, there is need to quantitatively determine its role on these variables to use it effectively in improving food security in these areas upon which the livelihoods of many rural dwellers depend.

As a result of fire, organic matter is consumed and mineral nutrients converted into inorganic forms, resulting in a temporary nutrient increase in the top soil layers (Skre et al 1998). Light and water conditions are also expected to improve in the short term after burning because of the reduction in competition due to tree seedling mortality and the general reduction in plant biomass (Skre 1985). Kimmins (1997) states that

this enhanced nutrient availability may occur after several years in deeper soil layers due to leaching. On the other hand, loss of organic soil structure may reduce the soil water holding capacity (Mallik 1986), and soil temperatures and evaporative loss may increase due to increased solar radiation and soil exposure (Skre et al. 1998).

3.1.5 Objectives and hypothesis

The main objective of this study is to investigate the long-term effects of frequency of burning on light interception, leaf area index and aboveground primary productivity of herbaceous vegetation in a South African semi arid savanna.

Key questions to be addressed were:

- How does fire frequency affect light interception and leaf area index?
- How does long-term fire frequency affect aboveground herbaceous plant biomass?
- What are the relationships between primary productivity, LAI and fIPAR in burnt semi-arid savannas?

The null hypothesis tested was that fire frequency has no effect on fIPAR, LAI and aboveground plant biomass .

3.2 Material and Methods

3.2.1 Measuring light availability using PAR Ceptometer

The study was conducted on a long term fire experiment at Fort Hare Research farm near Alice in the Eastern Cape Province, South Africa (32° 47' S; 27° 01' E). The vegetation is a semi-arid bush-clump savanna consisting of grassland, thickly interspersed with subtropical deciduous shrubs dominated by *Acacia karroo*, and is described by Acocks (1975) as the False Thornveld of the Eastern Cape. The long-term trial has been described in detail in Chapter 2.3. PAR irradiances and LAI were measured using a Decagon AccuPAR (Model PAR-80) ceptometer. The instrument is used to record ground measurements of photosynthetically active radiation (PAR) transmittance and these are used to indirectly derive LAI values based on the Beer-Lambert law for exponential light extinction in plant canopies (Serrano et al. 2000). The measurements were obtained on cloudless days in April and 2006 and December 2006 between 11h45 and 13h30. Sampling was done manually by recording the PAR readings above and below grass canopy. For each plot, twelve readings were recorded. The fraction of intercepted PAR fIPAR was calculated using the aforementioned formula $(1-I/I_0)$, then converted to percentages, while the summary of the corresponding LAI indices were computed by the device using the formula:

$$I/I_0 = \exp(-K \times LAI)$$

Where:

I is the irradiance at the depth z from the top of the canopy,

I₀ is irradiance at the top of the canopy,

LAI is the projected Leaf Area Index, and

K the leaf extinction coefficient for PAR.

3.2.2 Determination of aboveground biomass production

The standing crop of herbaceous vegetation was sampled from the 12 experimental plots in July 2006 before burning. For each plot, twelve samples were collected randomly by harvesting all standing livemass of herbaceous material within 1 m² quadrats at ground level using grass sickles. Twelve samples were harvested from

each of the twelve plots, which were considered as reasonable representative samples for the 100 m x 50 m plots. All dead or moribund material was set aside and not considered in the sampling. The harvested samples were placed in brown paper bags and oven dried to constant mass at 60 °C. The dry masses were used to calculate aboveground biomass production (g/m^2) for each treatment. All burning treatments coincided in August 2004 (Table 2.1) so that (except for the no burn plots) all the plots grew from a clean start for the 2004/2005 season. Only the annual burn was applied in August 2005, while the control treatment had not been burnt for 26 years. The annual and monthly rainfall varies from year to year, and the annual rainfall recorded for the area in the years 2005, 2006 and 2007 was 533 mm; 742 mm and 506 mm respectively (Figure 3.1).

3.2.3 Data analysis

After testing for normality, treatment effects on incident PAR, fPAR, LAI and aboveground biomass were tested by a one-way Analysis of Variance (ANOVA), where Means differing significantly (as indicated by the F-test) were separated using the Least Significant Difference (LSD) test at a 5 % level of probability. The fIPAR and LAI were regressed onto each other and also onto aboveground biomass using curvilinear models where the relationship was not linear to test the relationships between these variables.

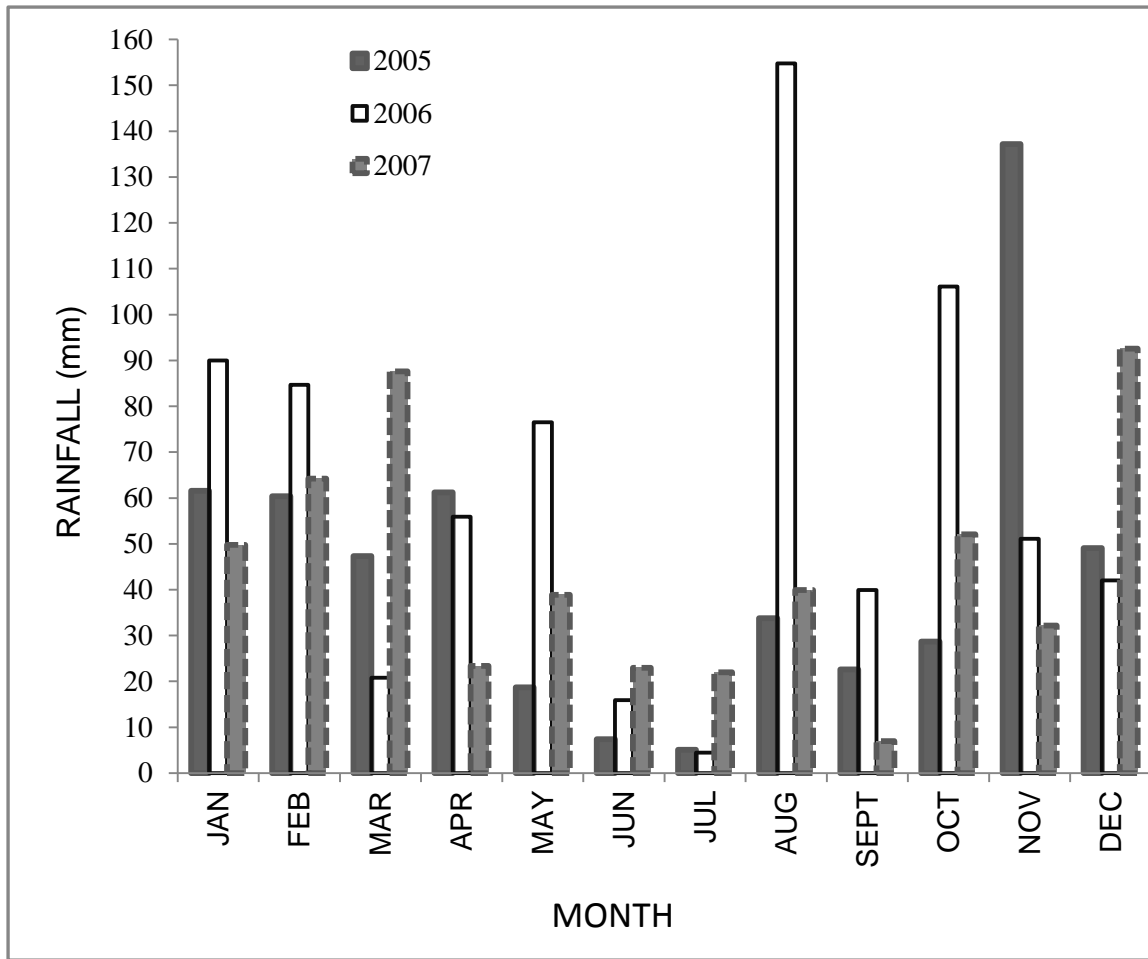


Figure 3. 1 Monthly rainfall recorded at Honey Dale section of the University of Fort Hare research farm in 2005, 2006 and 2007.

3.3 Results

3.3.1 Effect of fire frequency on PAR above and below canopy

Fire frequency had a significant effect on incident PAR measurements taken below the grass canopy ($P \leq 0.05$; $n = 44$), while above canopy PAR measurements were not significantly different ($P > 0.05$). The highest PAR readings below grass canopy were recorded in the frequently burnt plots (annual and biennial burns), while the lowest were recorded in the control and triennial burns (Table 3.1).

Table 3. 1 Mean (\pm SE) PAR readings for a long-term fire trial at the University of Fort Hare ($n = 24$; $P \leq 0.05$).

Treatment	Above canopy (MJ/m²/yr)	Below canopy (MJ/m²/yr)
Annual	1931 (99)	1011 (448) ^a
Biennial	1866 (36)	738 (175) ^a
Triennial	1897 (67)	369 (194) ^b
Quadrennial	1592 (238)	451 (112) ^b
Sexennial	1794 (36)	434 (132) ^b
No burn	1903 (72)	376 (187) ^b

*Means in the same column with different letters are significantly different ($P \leq 0.05$; $n = 44$).

3.3.2 Effect of treatments on fIPAR, LAI and aboveground biomass

Burning frequency had significant effects on the mean fraction of intercepted photosynthetically active radiation (fIPAR) and Leaf Area Index (LAI) ($P \leq 0.05$). The more frequently burnt plots (annual and biennial) had lower fIPAR and LAI values; while the less frequently burnt and unburnt plots had higher fIPAR and LAI values (Table 3.2). Quadrennial burns had lower fIPAR and LAI values than triennial burns, and moreover, the triennial values were the ones closest to the no burn controls as shown in Table 3.2. Aboveground biomass was also significantly affected by the

burning treatments ($P \leq 0.05$). The highest mean biomass was recorded in the triennial burn (306 g/m^2) while the lowest was recorded in the annual burn (192 g/m^2). Except for the annual and biennial burns, all other fire treatments resulted in a significantly higher aboveground biomass production than the no burn control treatment (Table 3.2). Although annual burn had the highest mean incident PAR below grass canopy, the percentage of intercepted PAR was the lowest probably because shorter burning intervals do not allow enough leaf area for light capture.

Table 3. 2 Mean (\pm SE) fIPAR and LAI for a long-term fire trial at the University of Fort Hare.

Treatment	%IPAR	LAI	Biomass(g/m^2)
Annual	48 (12) ^a	1.4 (0.5) ^a	192 (19) ^a
Biennial	63 (7) ^{ab}	2.3 (0.3) ^{ab}	222 (11) ^a
Triennial	80 (8) ^c	4.1 (1.2) ^c	306 (35) ^{bc}
Quadrennial	71 (1) ^{bc}	2.5 (0.4) ^{bc}	258 (2.8) ^b
Sexennial	76 (5) ^{bc}	3.1 (0.4) ^{bc}	282 (19) ^{bc}
No burn	80 (8) ^c	4.1 (1.2) ^c	214 (18) ^a

*Means along the same column with different letters are different ($P \leq 0.05$; $n = 24$).

3.3.3 The relationship between fIPAR and LAI as influenced by fire frequency

LAI increased linearly with increase in fIPAR as fire frequency decreased (Figure 3.2). The no burn control, triennial and sexennial burns resulted in higher LAI values, while annual, biennial and quadrennial burns had lower LAI values.

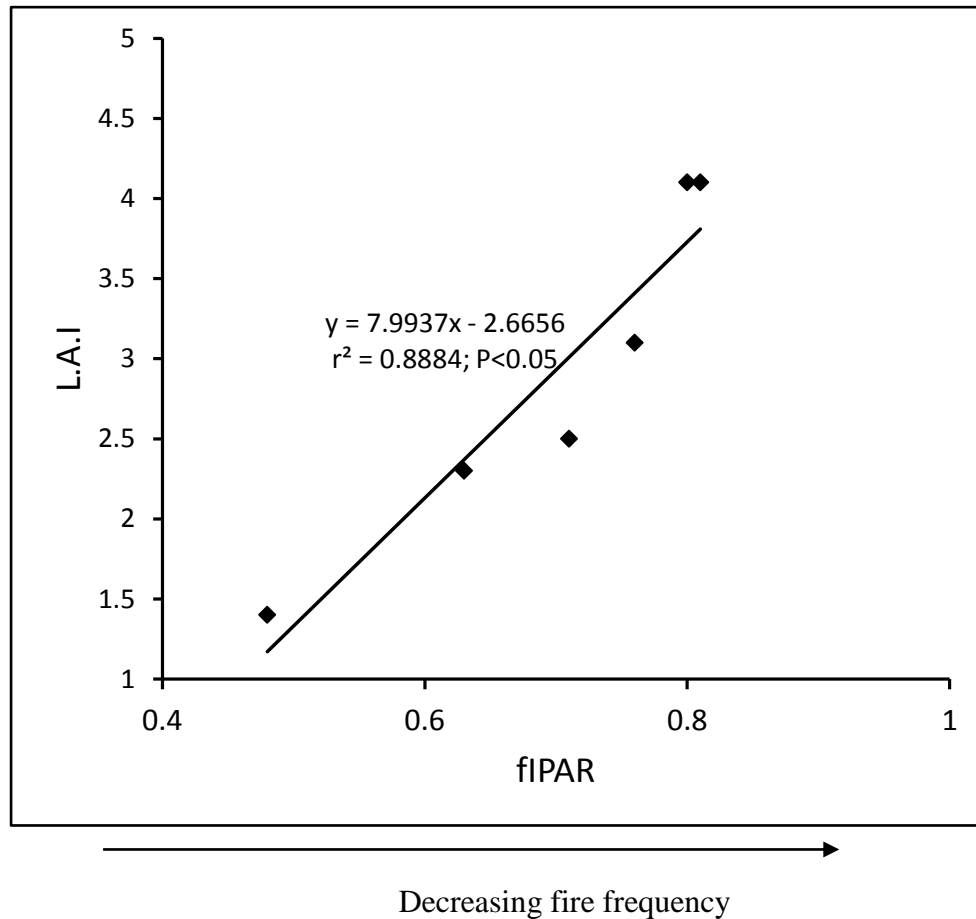


Figure 3. 2 Changes in LAI in relation to fIPAR across fire treatments (($P \leq 0.05$))

3.3.4 The relationship between %IPAR and biomass production as influenced by burning frequency

There was no linear relationship, but a weakly positive polynomial correlation between the fraction/percentage of intercepted PAR and aboveground biomass production ($r^2 = 0.58$; $P \leq 0.05$). As fire frequency increased (annual and biennial), both the percentage of intercepted PAR and biomass production decreased, and increased with less frequent burns fire frequency (sexennial and no burn) as shown in Figure 3.3. A significant polynomial relationship was also observed between LAI and aboveground biomass (Figure 3.4).

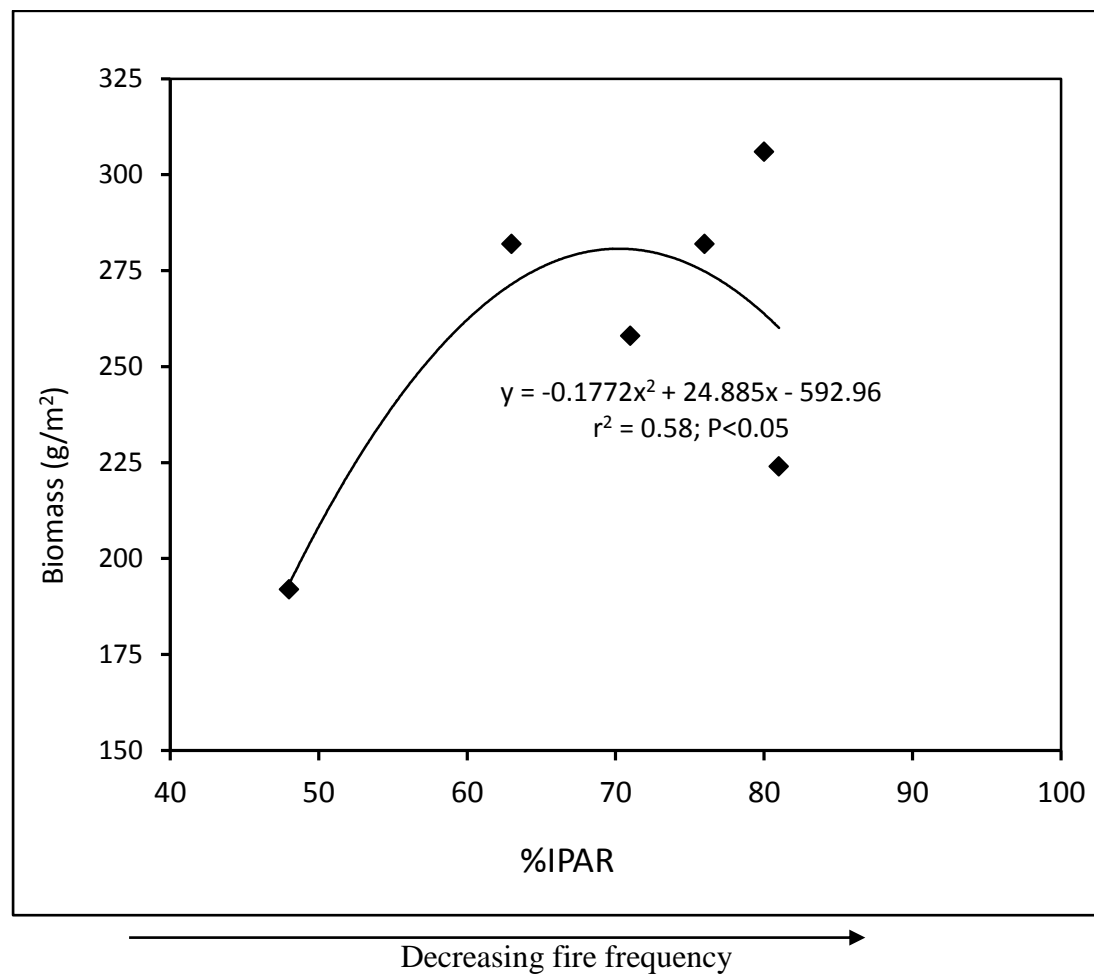


Figure 3. 3 Relationship between %IPAR and aboveground biomass as influenced by burning frequency ($P \leq 0.05$).

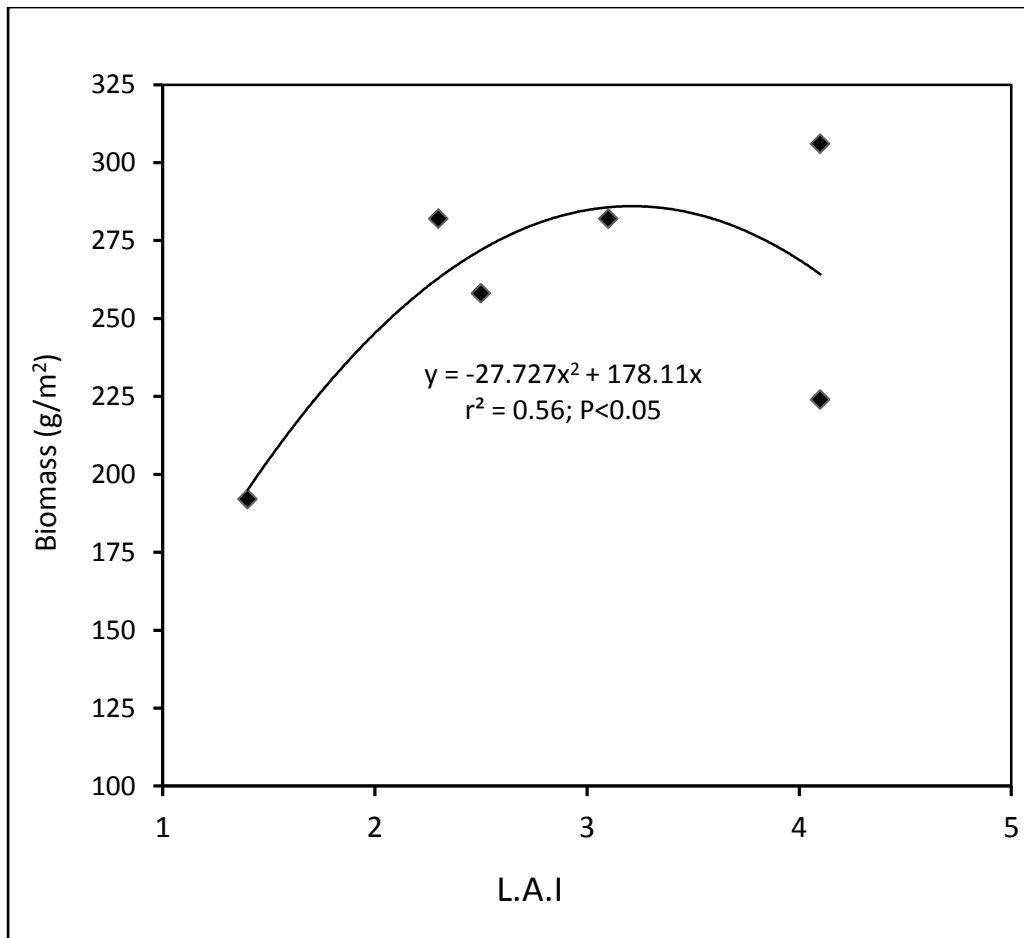


Figure 3. 4 Relationship between LAI and aboveground biomass as influenced by burning frequency ($P \leq 0.05$)

3.4 Discussion

3.4.1 Effect of fire frequency on light interception and Leaf Area Index

While there are concerns about fire effects on boreal forests (e.g. Rhyan 1991), it may be of benefit to temperate and sub-humid grasslands and savannas (Ansley et al. 2002) depending on fire regimes. In this study, frequent fire and its absence resulted in the lowest light interception and Leaf Area Index, while less frequent fire (primarily three-year burn) resulted in the highest LAI and light interception. These results are in conformity with those obtained by Knapp (1984), who demonstrated the importance of fire in creating a favourable microclimate environment for improved light interception, leaf temperature and water potential for the dominance of *Andropogon gerardii*. The implication is that in a semi-arid savanna, long fire intervals can improve conditions for improved light interception and improved re-growth by removal of litter and standing dead herbage, enhanced nutrient cycling and reducing competition for enhanced productivity of less shade tolerant herbaceous species. Frequent burning (e.g. annually or biennially) could improve conditions for light penetration, but the disadvantage (just like overgrazing) would be reduction in plant vigour. This would subsequently result in the plants not having enough leaf area to intercept the light, hence the resultant low biomass production.

3.4.2 Effect of fire frequency on biomass production of herbaceous plants

The three year burning treatment resulted in the highest aboveground biomass production, and these results are in agreement with the ones obtained by Skre (et al. 1998) in their studies with common forest plants in Norway. High biomass production in longer fire intervals may be attributed to improved nutrient and light penetration conditions as well as warmer temperatures near the soil surface after a fire (Trabout 1991; Heisler et al. 2004). Many of the dominant palatable grasses such as *Themeda triandra* and *Digitaria eriantha* are fire tolerant and need improved conditions for light interception at ground level to remain productive. In a study conducted by Trabout (1991) in the Mediterranean region, frequent fire greatly reduced tree density and phytomass while promoting herbaceous biomass production. Promotion of grass dominance is vital in range management of the False Thornveld of the Eastern Cape

for improved livestock production since the area is severely encroached by bush, mainly *Acacia karroo* (Trollope, 1983; Teague 1989).

Low primary production in frequently burnt areas may also be attributed to profound effects that fire has on soil seed banks. Soil seed banks play a major role in vegetation recovery after a disturbance (O'Connor 1996; Luzuriaga et al. 2005), and this also contributes to post-fire biomass productivity. Studies have indicated that frequent burning consumes most of the seeds found in the litter, upper and middle soil layers (Tesfaye et al. 2004; Snyman 2005), resulting in reduced germination and hence less biomass production as was observed in the annual and biennial burns. The absence of fire also creates intense competition for light and other resources, resulting in less shade-tolerant species becoming less productive.

3.4.3 Relationship between light interception, LAI and biomass production as influenced by burning frequency

From the results in Figures 3.3 and 3.4, one can deduce that an increase in leaf area index improved light interception, and this subsequently increased aboveground biomass production. Regression results showed that primary production increases with increase in LAI. Arias (et al. 2007) also found a strong relationship between calibrated LAI and stand yield of dominant tree species in Costa Rica. This confirms the statement that LAI is a key parameter in determining and monitoring primary production (Serrano et al. 2000; Myeni et al. 2002) and modelling of other ecological processes. However, despite the fact that the no burn treatment had the highest %IPAR and LAI (same as triennial burn), it resulted in the lowest biomass production. Also, though non-linear, the polynomial correlation between LAI and biomass production was also significant ($r = 0.56$; $P \leq 0.05$). This indicates that primary production is also affected by other environmental factors at play, and in complex systems such as savannas, their interaction may provide more practically meaningful results than the individual effects.

The rate of change of biomass depends on soil moisture, mortality, consumption rate of grazers, and fire effects (van Langeveld et al. 2003). In their study, van Langeveld (et al. 2003) found an enormous biomass increase in both burned and unburned plots

with an increase in rainfall in a Tanzanian savanna. (Trollope (1983) also highlighted that factors such as overgrazing, drought and frost complicate the interpretation of results ascribed to the response the vegetation to a particular burning treatment. For effective and sustainable use of fire in the management of these areas, a more holistic approach is required from studies conducted in relevant various fields of study for similar ecological zones.

3.5 Conclusions

This study has shown that high fire frequency or the absence thereof, reduces light interception and biomass production in the False Thornveld of the Eastern Cape. The hypotheses that fire frequency has no significant effect on fIPAR, LAI and aboveground biomass production is therefore rejected. Based on the results, optimum light interception and biomass production can be achieved by burning every three to four years because rejuvenation by fire maintains a higher level of productivity in semiarid savannas. These results are also in conformity with the recommendations made in Chapter 2.5, indicating that not only do they appear to support maintenance of biodiversity, but also the system's productivity. However, other key factors such as rainfall and season of burn should be taken into consideration when using fire as a management tool in grasslands and savannas due to the role of interaction in these ecological systems. Moreover, these results were obtained in the absence of grazing, and where grazing is applied, longer fire intervals would be recommended, or when there is no accumulation of moribund herbage due to constant defoliation by grazers, burning may not be necessary. In that case, fire should be avoided until such time that the vegetation has sufficiently recovered and accumulated enough fuel load. It is recommended that for the restoration of degraded savannas, fire should be avoided because it will exacerbate the problem of reduced grass cover and negatively affect exposed soil seed banks.

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CHAPTER 4 EFFECTS OF LONG-TERM BURNING FREQUENCY ON SOIL NUTRIENTS IN THE FALSE THORNVELD OF THE EASTERN CAPE

Abstract

The effects of burning frequency on soil nutrients and nitrogen mineralization were determined in the upper surface soils of a South African semi-arid savanna. The test hypothesis was that burning frequency has no effect on N mineralization and soil nutrients. The study was conducted on a long-term fire experiment that was established in 1980 at the University of Fort Hare research farm (32° 47' S; 27° 01' E). Treatments included annual, biennial, triennial, quadrennial and sexennial burns and a no burn control, all replicated twice on 50 m x 100 m plots. Soil samples were collected in August 2006 at four different depths (0-2; 2-4; 4-6 and 6- 8 cm respectively) and analyzed for pH, total C, N, P, K, Ca, Na and the C: N ratio. Nitrogen mineralization was determined in 2007 by adopting the in situ buried ion-exchange resin bag technique.

Burning treatments and soil depth had no significant effect on pH, N, P, K, Ca, Na and the C: N ratio, but deeper soils had significantly lower total carbon concentrations. Though statistically not significant, trends indicate that fire frequency increased soil pH, Ca, K and Na, but decreased total C, N and P. Total C, N, Ca and P decreased with depth, while pH and K increased. Treatment means for pH at the 6-8 cm depth were significantly higher than control means at all depths (except the 4-6 cm depth in the triennial burn, while all treatment means for all treatments at all depths were significantly lower than those of the no burn treatment. Burning frequency significantly decreased N mineralization, and all the treatment means for the burnt plots were significantly lower than those of the no burn control. There was no significant correlation between pH and total C, Ca, C:N ratio, Na and P, but had a positive correlation with K and negatively correlated with total N. There was a negative correlation between burning frequency and N mineralization ($r = -0.74$; $P \leq 0.05$). N mineralization had no significant correlation with total N, total C or the C: N ratio. The results highlight the complexity of burning in semi-arid rangelands fact that

frequent burning can lead to a reduction in some soil nutrients such as C N and P, while increasing others such as Ca and Na.

Keywords: Burning frequency, N mineralization, nitrification, soil depth, soil nutrients, semi-arid savanna.

4.1 Introduction

Provision of adequate soil-based nutrients is vital for the growth of individual plants and communities making up natural ecosystems as well as agricultural production systems. Plants suffer nutrient deficiency stress when the availability of soil nutrients (and/or the amount of nutrients taken up) is lower than required for sustaining metabolic processes in a particular growth state (Regel and Marschner 2005). These nutrients are heterogeneously distributed spatially and temporally because of environmental and climatic factors which directly or indirectly affect their availability to plant life. Studies have indicated that growth of individual plants can be increased by several folds with different patterns of nutrient supply (Wijesinghe et al. 2005). Soil fertility has many facets and is defined in relation to its use (Gregorich et al. 1994), and according to Mills and Fey (2004), any decline in soil fertility implies misuse of soils.

Livestock production is a major contributor to the livelihoods of many households in African grasslands and savannas. In semi-arid grasslands and savannas where economic and environmental issues are challenging, prudent management of mineral resources becomes a priority (Carter 2006; Stroia et al. 2007). The effects of inappropriate land use practices in South Africa have been a subject of debate for decades (Scott 1947; 1970; Donaldson 2002; Mills and Fey 2004). The focus has been mainly on soil erosion and restoration policies focused primarily on its control (e.g. The Soil Conservation Act of 1946). Nutrient management is a key component to sustainable agriculture (Carter 2006). A proper understanding of how soil properties may be affected by different land use practices is a precursor to managing the soil resources effectively.

Most of the semi-arid savannas of the Eastern Cape are used for livestock grazing. Fire occurs naturally in these ecosystems and is consequently widely used as a management tool for various purposes such as improving forage quality and palatability (FORIG 2003; Archibald et al. 2005). Farmers frequently burn rangelands irrespective of the amount of ungrazed material remaining from the previous season (Teague et al. 1984). This is done because re-growth on burnt veld is more acceptable to grazing animals than the re-growth of vegetation which has been defoliated either

by grazing or mowing (Materechera et al. 1998). Post-fire re-growth is considered more nutritious because it is not contaminated by low-quality residual material from previous seasons (Mentis & Tainton 1984). Moreover, post-fire growth is also reported to have higher protein and mineral content resulting from mineralization during combustion (Stock and Lewis 1986). However, there is a lack of general consensus on the impacts of season and frequency of burning, which often arise because objectives of burning are often in dispute (Tainton 1999). These controversies highlight the need to quantitatively evaluate the short, medium and long-term effects of fire on soil characteristics to get a deeper insight of how fire affects vegetation performance and sustainability of livestock production.

4.1.2 The role of macro and micronutrients in plant growth and performance

Soil minerals exist in many forms, some of which are complex and difficult to quantify. These minerals exist in organic and inorganic forms, and are distributed throughout the aqueous and solid media, as well as in living tissues of soil biota. They come into the ecosystem in rain and dust, by biological fixation of organic matter and weathering of rocks, and go out through leaching and in gaseous form through denitrification and volatilization by fire (Attiwill and Adams 1993). Some nutrients such as nitrogen, phosphorus, calcium, magnesium and sulphur are required in larger quantities, compared to other essential elements such as copper, iron, molybdenum, sodium and zinc which are referred to as micronutrients. Irrespective of their required quantities, any short supply can result in deficiencies, which indicate some form of improper malfunction. Soil fertility of drier savannas is mostly related to the availability of nitrogen and phosphorus. Calcium, magnesium, potassium and sodium are generally not thought to be very limiting in dry savannas, but they could become limiting in wetter savannas because they can be lost through leaching (Scholes and Walker 1993).

Carbon, nitrogen, phosphorus and sulphur are intimately bonded together and form part of the plant protoplasm. Carbon content of soils is important because it is the main energy source for heterotrophic organisms that convert organic matter into soil humus for the nutrients required by plants (Coleman et al. 1983; Gan et al. 2009). Nitrogen is a part of all living cells and is essential for numerous functions such as

formation of amino acids, proteins and metabolic processes involved in the transfer of energy. An adequate supply of nitrogen is associated with vigorous growth, a deep green colour, increase in seed and fruit formation and improved foliage and crop quality (Tisdale and Nelson 1975). The concentrations of carbon and nitrogen in the soil are positively correlated with plant biomass, and also with each other (Hogberg, 1986). The C: N ratio for most soils ranges from 10 to 15 (FAO-UNESCO 1977), which is generally perceived to be adequate to allow a fairly rapid turnover of soil organic matter. When plants are deficient in nitrogen, they suffer from chlorosis and stunted growth. Insufficient nitrogen supply also leads to deposition of carbohydrates in vegetative cells causing them to thicken, instead of proteins being manufactured (Alberta Agriculture, Food and Rural Development 1998).

Phosphorus is usually the second most limiting factor for grass production after nitrogen (Aerts and Chapin 2000; Stroia et al. 2007). Phosphorus plays a crucial role in the energy transfer processes in both aerobic and anaerobic life processes. Organic phosphate compounds are essential for photosynthesis, carbohydrate inter-conversion, glycolysis, amino-acid and fat metabolism, sulphur metabolism, biological oxidations and ontogenic processes such as root growth, seed formation and proper maturation (Tisdale and Nelson 1975). Potassium does not form part of the plant protoplasm, but is nonetheless a macronutrient essential for carbohydrate and nitrogen metabolism as well as protein synthesis. It is also, among other roles, responsible for the control and activities of various enzymes and essential elements, photosynthesis, plant immunity, as well as the adjustment of stomatal movement and plant water relations (Alberta Agriculture, Food and Rural Development 1998).

Plants also need an adequate supply of micronutrients such as iron, zinc and sodium, failing which some deficiency symptoms may occur. Calcium is an essential component of cell wall structure, provides for normal transport and retention of other elements as well as strength in plants. It enhances protein synthesis, and is also involved in carbohydrate translocation as well as chromosome stability (Tisdale and Nelson 1975). Its deficiency results in failure of terminal buds and root apical meristems to develop.

4.1.3 The importance of Soil pH

Soil pH, a measure of the acidity and alkalinity of soil, has profound effects on soil mineral solubility, since fourteen of the seventeen plant essential nutrients are obtained from the soil solution in dissolved form. Most of the nutrients are more soluble in slightly acidic (pH between 6 and 7) than neutral or more alkaline soils, but too much soil acidity (pH below 5) can lead to heavy metal toxicity. In general, macronutrients tend to be less available in soils with low pH, while micronutrients become less available in soils with high pH (Alberta Agriculture, Food and Rural Development 1998). Soil pH can also influence plant growth by its effect on the activity of beneficial microorganisms, hindering decomposition. In humid areas, soils may be acidic because bases are usually leached out, and the exchange complexes become saturated with hydrogen ions and aluminium, lowering soil pH (Boerner 1982). On the other hand, the topsoil in arid areas may be more alkaline due to the accumulation of bases, while semi-arid areas will form an intermediary between these two scenarios. However, Hogberg (1986) highlights that the liberation of base cations during fires in savannas causes a transient increase in soil pH. However, Mills and Fey (2004) reported contrasting results in that annual burn decreased soil pH in some experiments, but increased it in others. These reports indicate the need for further investigation.

4.1.4 Effects of fire frequency on soil nutrient status

Vegetation enriches soil surface horizons with nutrients through litter, trapping of dust or by providing cover for birds and mammals (Bolton et al. 1993; Scholes and Archer 1997; Allsopp 1999). Disturbances such as fire can cause changes in both scale and intensity of the factors that influence community and ecosystem functioning (Rice 1993) such as moisture and nutrient availability. Fire is a natural disturbance in many ecosystems of the world that has profound effects on ecosystem dynamics. Grasslands and savannas are normally fire dependent ecosystems (Myers 2006). The role of fire on African grassland and savanna ecosystem structure and function is the oldest in their ecology, but certain aspects still remain contentious to date, such as frequency of burn and its effects on soil nutrient availability. Despite all the controversy surrounding whether fire improves soil nutrient status, prescribed burning is still a management tool for livestock production and nature conservation many ecosystems

of southern Africa (Trollope et al. 1998; Archibald et al. 2005; Manson et al. 2007), and there are also uncontrolled fires that influence fodder flow planning in these areas (Snyman 2003). Frequency of burn is the most challenging of the four aspects of a fire regime due to the highly variable rainfall and biomass accumulation patterns in these areas.

In the absence of fire, vegetation can either be consumed by herbivores, or may in time return to the soil surface and be decomposed by microbes. During the dormant winter period (June to August), large areas of southern African semi-arid rangelands are also subjected to large-scale fires, which are either planned or unplanned. Fire dramatically alters nutrient cycling through volatilization, substrate transfer in the form of particulate matter, smoke and ash as well as by inducing nutrient losses and leaching (Driscoll et al. 1999). Fire could significantly therefore contribute towards the distribution of nutrients in rangelands by rapidly mineralizing above-ground biomass and depositing nutrients as ash and charcoal onto the soil surface (Materechera et al. 1998). Depending on soil texture and post-fire climatic conditions, these nutrients may or may not be incorporated into the soil profile. The aforementioned authors also raised a concern of the high losses of nitrogen and sulphur during combustion of organic matter, and this calls for a more critical evaluation of medium to long-term effects of fire as a management tool in drier areas, especially its frequency.

Some studies have indicated that soil organic matter (SOM) tends to decline in landscapes that are burnt regularly (e.g. Jones et al. 1990; Bird et al. 2000), and this has been attributed to increased mineralization of soil organic matter as well as reduced inputs of soil organic matter due to combustion of above-ground biomass and litter (Mills and Fey 2004). This may be an indication that the decision to burn should be based on specific management objectives in time and in space, as well as prevailing conditions. Charcoal additions to soil have been shown to increase soil fertility and pH in Brazilian Amazon (Glaser et al. 2002; Kurth et al. 2006.). In semi-arid savannas, fire also increases water stress by increasing evaporative loss through removal of standing vegetation which then exposes the topsoil to excessive heat. Burning also increases plant mortality because some species that are not fire-tolerant become less abundant or may gradually disappear in burnt areas (Redman et al. 1993).

This can also affect soil chemistry and nutrient availability to plants. In this semi-arid savanna soil moisture and soil nutrients are the key environmental variables that regulate productivity and relative abundance of vegetation (Huntley 1982; Mworira et al. 2008).

There is a consensus that fire has a considerable effect on nutrient cycling, but there are some contrasting reports on the effect of fire on soil nutrient pools. Some studies reported a post-fire flush of nutrients such as P, K Ca and Mg (Tomkins et al. 1991; Stromgaard 1992; Blank and Zamudio 1998; Brown and Smith 2000). While there is often a short-term increase in nitrogen availability after a fire due to ammonium and nitrate ions found in ash, there are also some reports of considerable loss due to volatilisation (Stock and Lewis 1986; Choromanska and DeLucia 2001). Some studies reported a positive correlation between fire frequency and foliar nitrogen, zinc and copper concentrations (Brown and Smith 2000; Ferweda et al. 2006), while others found a reduction in structural carbohydrates (Bryant et al. 1983; Cole 1988). A decrease in structural carbohydrates causes an increased demand for carbon for biomass production due to increased nitrogen availability (Bryant et al. 1983). This scenario indicates the importance of nutrient balance (e.g. the C: N ratio), and this principle applies to all essential elements because the proportion or concentration of one nutrient may affect uptake or utilization of another.

4.1.5 Nitrogen dynamics in natural ecosystems

Soil nutrient dynamics are influenced by the rate of decomposition of organic matter (Tripathi and Singh 2009), which is also influenced by environmental factors and other soil chemical properties. Soil nitrogen is one of the most important factors that control ecosystem stability (Vitousek 1990; Evans et al. 2001). Nitrogen is an essential element for plant growth, and a key element of agricultural inputs such as fertilizers. Nitrification and nitrogen mineralization are the main processes responsible for nitrogen turnover in soils (Maly et al. 2002), and the major sink for nitrogen in mature vegetation types is usually in the soil organic matter (Nedelhoffer et al. 1999). In soils that have not been artificially unfertilized, nitrogen availability is largely determined by mineralization, which is defined as the microbial conversion of organic nitrogen to ammonium (Pastor et. al. 1984). Ammonium can be oxidized to

nitrate (a process called nitrification), and highly productive soils have a high potential to nitrify (Vitousek et al. 1982). Ammonification releases mineral ammonium N from soil organic matter, while nitrification converts ammonium N to mineral nitrate N. Net mineralized-N supplies most nitrogen to vegetation, except for N-fixing legumes and agricultural crops provided with more N for optimal yields.

Nitrogen mineralization is of prime importance in ecosystem productivity, and soil nitrogen transformations control nitrogen supply and losses from the ecosystem (Knoepp and Swank 2002; Milkha and Rice 2004). High C:N and lignin:N ratios in litter decrease net mineralization by increasing nitrogen limitations to microbial activity during decomposition (Evans et al. 2001). However, there are a number of ways by which plants can control nitrogen cycling, and these include atmospheric nitrogen fixation, sequestering certain amounts of N in plant biomass or by alteration of nitrogen distribution to aboveground and belowground plant parts (Vitousek et al. 1987; Lovett et al. 2004).

Long-term landscape health can be achieved if basic ecosystem services of capturing and recycling nutrients are maintained. In semi-arid savannas soil moisture and soil nutrients are the key environmental variables that regulate productivity and relative abundance of vegetation (Huntley 1982; Mwaria et al. 2008). Water and temperature are also recognized as factors that most limit net N mineralization and plant nitrogen availability in arid ecosystems (Vinton and Burke 1997), but once these two are adequate, quality of organic matter becomes the primary control (Burke 1989; Vinton and Burke 1997). Plant production is often limited by nitrogen availability in many ecological systems, and therefore nitrogen can be a sensitive indicator of ecosystem productivity and function (Attiwill and Adams 1993; Chapin et al. 2002).

Savanna landscapes used for livestock production characteristically experience natural disturbances such as grazing and fire, which can alter the ability of a landscape to retain water, nutrients and carbon. An understanding of how these factors affect key landscape processes such as moisture and nutrient availability in space and time, may help managers to make informed decisions and recommendations to maintain healthy and sustainable landscapes (Dawes-Gromadzki and Webb 2008).

4.1.6 Fire effects on nitrogen mineralization

The removal of vegetation increases soil temperature, thereby enhancing conditions for mineralization (Turner et al. 2007) if there is sufficient moisture. Among the major soil nutrients, nitrogen is likely to be the most sensitive to the impacts of fire (Carreira et al. 1994). Fire dramatically alters nitrogen availability in the short term through its immediate impact on organic matter pools (Clarke 1990). The processes which affect nitrogen cycling as a result of fire include volatilization, substrate transfer in the form of particulate matter, smoke, ash as well as by inducing nutrient losses and leaching (DeBano et al. 1998; Driscoll et al. 1999). Nitrogen dynamics in response to disturbance have hence received some considerable attention (e.g. Vitousek et al. 1979; Boerner 1982; Vitousek and Matson 1985; Attiwill 1993; Turner et al. 2007). Fire volatilizes nitrogen from vegetation and litter, thereby reducing its storage in the burned ecosystem, but it often increases mineralization of the remaining organic matter (Turner et al. 2007). Ammonium and readily decomposable organic nitrogen compounds added with ash deposition, along with post-fire temperature and moisture increases, may promote mineralization and nitrification (Raison 1979).

Studies on post-fire nitrogen pools in an array of ecosystems have revealed multiple-fold increases in NH_4^+ and NO_3^- that were short-lived. For example, Covington and Sackett (1992) and Wan et al. (2001) reported a 2 to 26-fold increases in soil NH_4^+ that lasted less than two years, and a 5-fold increase in soil NO_3^- following a stand-replacing fire. Fynn et al. (2003) reported a reduction in mineralizable N in a long-term burning experiment of a South African mesic grassland. It is therefore imperative to distinguish between short-term changes occurring after a single or several fire events and the long-term ecological effects resulting from different fire regimes such as intensity, frequency, season and type of fire. Most of the studies done on the role of fire on nitrogen dynamics were short-term experiments conducted in forest and temperate or Mediterranean systems and much less work has been done on other vegetation types. More studies are needed to quantify not only short-term effects, but also medium and long term post-fire nutrient pools in fire-prone ecosystems such as mesic and semi-arid grasslands and savannas.

4.1.7 Rationale and Justification for the studies

Many farmers in semi-arid systems of South Africa and elsewhere frequently burn rangelands with the aim to improve their livestock production by utilizing good quality post-fire re-growth (Schacht et al. 1996; Snyman 2003) without calculating the impact of the fire on the entire ecosystem functioning. Considering all the controversy and the increasing management concern for a net loss of soil organic matter (especially N) from the system, low forage production and erosion of surface soil, the need for further studies to understand the effects of fire on nutrient cycling and soil properties is 'critical' as stated by Manson (et al. 2007). Understanding of these changes will assist rangeland management decisions and ensure sustainable livestock production in these areas.

4.1.8 Objectives and hypotheses

The main objective of this study was to investigate the long-term effects of fire frequency on the soil fertility in a semi-arid savanna referred to as the False Thornveld of the Eastern Cape (Acocks, 1988). The specific objectives were to quantify the effects of burning on soil pH, organic matter, extractable P and exchangeable Ca, K, Na and N mineralization in the upper soil surface layer. The test hypothesis was that burning frequency has no effect on N mineralization, soil pH and soil nutrients.

4.2 Material and Methods

4.2.1 Study site

The study was conducted at a long-term fire experiment that was established in 1980 at the Honey-Dale section of the University of Fort Hare research farm (32° 47' S; 27° 01' E). The trial was set up to investigate the effects of burning frequency on species composition, basal cover and herbage production. The long-term experiment has been described in Chapter Two (2). Burning treatments include a no burn, annual, biennial, triennial, quadrennial and sexennial burn, and are replicated twice in a completely randomized design (Figure 2.1; Table 2.1).

5.2.2 Soil sampling

Soil samples were collected from a surface layer (0- 8 cm) in each of the twelve experimental plots in July 2007 after application of burning treatments. The cores were collected at four different depth intervals (0-2 cm; 2- 4 cm; 4-6 cm and 6 – 8 cm depths). These depths were chosen because of reports of burning-induced decrease in organic C in the 0-2 cm layer and a tendency for increase in organic and mineralizable C at lower depths (Fynn et al. 2003). Twelve samples were collected from each plot at each depth, and the samples were mixed to make four representative samples for each depth. After removal of roots and other plant material, the soil samples were air-dried to constant mass and milled to pass through a 2 mm sieve, then stored in glass sample bottles until analyzed.

4.2.3 Chemical analyses

Soil pH was determined using 1 M KCl and water at 1:1 soil-solution ratio using glass electrodes. Phosphorus was extracted with the Bray 1 solution and determined using a spectrophotometer as described by Bray and Kruz (1945). Plant available Ca, K and Na were extracted using standard methods of soil chemical analyses (Anon 1987; AOAC 1990). Total N and organic C were extracted from soil by the method of Gregorich and Ellert (1993) using Na solution (SG =7). Isolated light fraction material was prepared (oven-dried at 60°C, dried and weighed), then analyzed for organic C and total N.

Soil nitrogen mineralization was determined in 2007 by adopting the *in situ* buried ion-exchange resin bag technique (Binkley and Hart 1989; Blair 1997). Resin bags were used as relative indicators of NH_4^+ and NO_3^- leaching from the plots, hence plant N availability. Approximately 10 g of anion exchange resins (Dowex 1X8-50, 20-50 mesh) and 10 g of cation exchange resins (50WX8-40; Dowex HCR-W2, 8% cross linking, 16-40 mesh) were enclosed in small bags made from nylon stockings. The resins were charged by soaking them overnight in 0.5 M HCl, and then rinsed with distilled water. Eight bags were buried per plot at a 10 cm depth. Each bag was tied to a white-painted peg using a monofilament nylon fishing line prior to burial in soil. The bags were left in soil from October 2007 through April 2008, then retrieved from the plots. Some of the buried bags could not be retrieved due to damage of the nylon line by rats, or during digging. At least 5 bags were retrieved from each of the 12 plots (ie. 60 bags in total). They were then processed using 2 M KCl to determine N exchanged from the resin. The extracts were neutralized with 0.02 M NaOH, then run through an Alpkem autoanalyzer.

4.2.4 Data analyses

The effects of treatments on soil nutrient concentrations were tested on each variable using a two-way ANOVA after testing for all assumptions. The main factors used in the model were burning frequency and soil depth, as well as their interactions. Least Significant Difference tests were used to test differences between treatment means. Correlations were tested between soil pH and other properties. The data for soil pH were log-transformed due to large residuals, but they differed only slightly from untransformed, so the ones presented are for the untransformed data. Effects of burning treatments on N mineralization were tested by one-way Analysis of Variance, while differences on individual means were tested using the LSD test. Correlation between fire frequency and mineralized N was tested with the Pearson correlation coefficient test. Also tested were correlations between mineralized N and total N; Total N and the C: N ratios. GenStat 11 was used to conduct the analyses at $\alpha = 0.05$.

4.3 Results

4.3.1 Effects of treatments and depth on soil chemical properties

Soil depth had highly significant effect on total C ($P \leq 0.01$), while N, P, K, Ca, Na, soil pH and the C:N ratio were not significantly affected by either burning frequency or soil depth at ($P > 0.05$). Although all statistical tests were performed at $\alpha = 0.05$, the P-values (Table 4.1) indicate that most of the soil properties were very close to significantly affected by burning treatments at $\alpha = 0.05$. Soil depth also had significant effect ($P \leq 0.01$) on the soil variables except for Na and the C:N ratio. The interaction between burning frequency and soil depth did not have significant effect on any of the soil properties ($P > 0.05$).

Table 4. 1 P-values for a 2-way ANOVA for soil chemical properties

(n = 48; $\alpha = 0.10$).

Source	d.f.	pH	Ca	K	P	Na	N	C	C:N
Treatment (A)	5	0.718	0.485	0.718	0.485	0.072	0.919	0.338	0.934
Soil depth (B)	3	0.056	0.088	0.056	0.088	0.215	0.0530	0.000	0.168
A x B	15	0.994	0.659	0.994	0.659	0.745	0.832	0.441	0.566

The trends in soil properties as affected by burning frequency can be divided into two categories: those that increased with fire frequency, and those that decreased with increase in fire frequency. Frequent burning resulted in an increase in soil pH, K, Ca, and Na, while it decreased C, N, and P concentrations. The results of burning treatments on the soil properties are presented in Table 4.2, while those of the soil depth are presented in Table 4.3. Carbon concentrations generally decreased with increase in soil depth, with the highest recorded in the uppermost layer (0-2 cm), and the lowest (1.23) in the 6-8 cm depth. These two values also differed significantly. A similar pattern was observed with nitrogen, though the treatment means were not

significantly different (Figure 4.1). Soil pH and K generally showed an increasing trend with increase in soil depth, while Ca, P and N concentrations showed a declining trend. The mean C:N ratio was highest on the 0-2 cm depth and lowest on the 2-4 cm depth (Table 4.3).

Table 4. 2 Means (\pm SE) for the main effect of burning frequency on soil properties in a long-term fire experiment ($P \leq 0.05$; $n = 60$).

Treatment	pH	C (%)	N (%)	C:N ratio	Ca (mg/kg)	K (mg/kg)	P (mg/kg)	Na (mg/kg)
Annual	6.42 \pm 0.02	1.45 \pm 0.13	0.12 \pm 0.0	16.8 \pm 1.3	538 \pm 137	64.1 \pm 0.3	0.54 \pm 0.14	5.4 \pm 1.4
Biennial	6.39 \pm 0.01	1.75 \pm 0.17	0.13 \pm 0.01	16.0 \pm 0.8	516 \pm 116	63.9 \pm 0.1	0.52 \pm 0.12	5.2 \pm 1.2
Triennial	6.41 \pm 0.01	1.6 \pm 0.02	0.10 \pm 0.02	16.7 \pm 1.5	311 \pm 89	64.1 \pm 0.3	0.31 \pm 0.09	3.1 \pm 0.12
Quadrennial	6.40 \pm 0.01	1.56 \pm 0.02	0.13 \pm 0.01	14.0 \pm 0.8	336 \pm 64	64.1 \pm 0.3	0.34 \pm 0.06	3.4 \pm 0.9
Sexennial	6.36 \pm 0.04	1.51 \pm 0.05	0.14 \pm 0.01	14.9 \pm 0.8	294 \pm 106	63.7 \pm 0.1	0.29 \pm 0.11	2.9 \pm 0.11
No burn	6.29 \pm 0.11	1.62 \pm 0.04	0.14 \pm 0.04	14.9 \pm 0.6	410 \pm 10	62.9 \pm 0.9	0.41 \pm 0.01	4.1 \pm 0.1

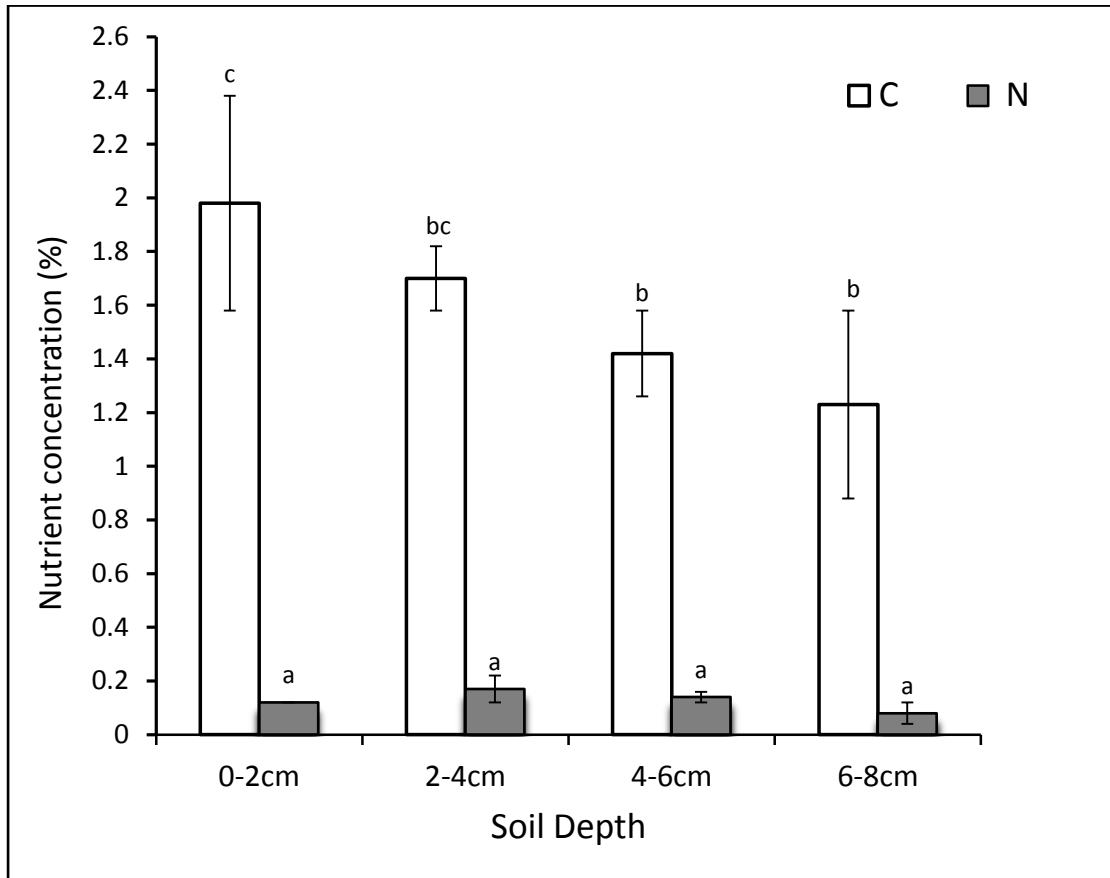


Figure 4. 1 Means (\pm SE) for the effect of soil depth on C and N concentration in a long-term fire experiment. Means with the same letters are not significantly different ($P > 0.05$).

Table 4. 3 Means (\pm SE) for the effect of soil depth on soil properties in a long-term fire experiment.

Depth (cm)	pH	C:N Ratio	Ca (mg/kg)	K (mg/kg)	P (mg/kg)	Na (mg/kg)
0-2	6.29(0.11) ^a	18.0(2.5) ^c	609(208) ^c	62.9(1.7) ^a	0.61(0.21) ^c	6.09(2.1) ^c
2-4	6.34(0.10) ^a	12.5(3.0) ^a	358(14) ^b	63.4(0.1) ^a	0.36(0.04) ^b	3.58(0.4) ^b
4-6	6.41(0.01) ^b	14.4(1.1) ^b	333(68) ^{ab}	64.1(0.3) ^{ab}	0.33(0.07) ^{ab}	3.33(0.7) ^{ab}
6-8	6.48(0.04) ^b	17.1(1.6) ^{bc}	302(99) ^a	64.8(0.4) ^{ab}	0.30(0.04) ^a	3.02(1.0) ^a

*Values with different letters in the same column are significantly different ($P \leq 0.05$)

4.3 2 Interactive effects of fire frequency and soil on chemical properties

Post-hoc (LSD) analyses also revealed some observable trends in the soil properties. The triennial and quadrennial burns resulted in the highest mean pH (6.57), while the no burn treatment resulted in the lowest mean pH of 6.06 in the uppermost layer (Table 4.3). Mean separation revealed significant differences between the pH values for the no burn uppermost layer and the annual 4-6 and 6-8 cm layers. The pH for the no burn uppermost layer was also significantly lower than those of the 6-8 cm layers in the biennial 6-8 cm; triennial, quadrennial and sexennial burns (Table 4.4) Except for potassium, the concentrations of all the other nutrients decreased with increase in soil depth across all the burning treatments, with the highest mean values mostly recorded in the no burn treatment (Table 4.4). Calcium and phosphorus concentrations were highest on the 2-4 cm layer in the annual burn treatment. Potassium concentrations portrayed an opposite pattern by increasing with increase in soil depth. The highest value of 65.6 mg/kg K was recorded at the 6-8 cm depth in the triennial and quadrennial burns, while the lowest was at the topmost layer in the no burn treatment (Table 4.4). The no burn treatment in the topmost layer resulted in the highest C concentration, which differed significantly from all the other treatment means (except the uppermost biennial and triennial burns). The topmost layer in the no burn treatment had the highest C:N ratio (23.2), which was significantly higher than the 2- 4 cm layer in the quadrennial burn, as well as the 4- 6 cm layer in the no burn and annual burns respectively. All the treatment means for total N were not significantly different at 5 % (Table 4.4).

Table 4. 4 LSD test results for soil mineral concentrations at different levels of depth in a long-term fire experiment . Means with the same letter in a column for each depth are not significantly different ($P \leq 0.05$; $n = 60$).

Treatment	pH	Total C (%)	Total N (%)	C:N ratio	Ca (mg/kg)	K (mg/kg)	P (mg/kg)	Na (mg/kg)
0-2 cm								
No burn	6.09 ^a	2.48 ^d	0.12 ^a	23.2 ^a	690 ^b	60.9 ^a	0.69 ^b	6.90 ^c
Annual	6.31 ^a	1.52 ^b	0.08 ^a	22.4 ^a	1280 ^c	63.1 ^a	1.28 ^b	2.75 ^a
Biennial	6.40 ^a	2.04 ^c	0.11 ^a	19.4 ^a	660 ^b	63.7 ^a	0.66 ^b	6.60 ^c
Triennial	6.31 ^a	2.08 ^c	0.13 ^a	16.7 ^a	405 ^a	63.1 ^a	0.41 ^a	4.05 ^{bc}
Quadrennial	6.35 ^a	1.92 ^{bc}	0.15 ^a	13.1 ^a	310 ^a	63.5 ^a	0.31 ^a	3.10 ^a
Sexennial	6.34 ^a	1.84 ^{bc}	0.14 ^a	13.2 ^a	320 ^a	63.4 ^a	0.31 ^a	3.10 ^a
2-4 cm								
No burn	6.28 ^a	1.69 ^b	0.16 ^a	12.1 ^a	375 ^a	62.8 ^a	0.38 ^a	3.75 ^b
Annual	6.43 ^b	1.52 ^b	0.14 ^a	13.3 ^a	280 ^a	64.3 ^a	0.28 ^a	2.80 ^a
Biennial	6.40 ^a	1.86 ^{bc}	0.21 ^a	11.8 ^a	425 ^b	63.7 ^a	0.43 ^a	4.25 ^{bc}
Triennial	6.32 ^a	1.71 ^{bc}	0.10 ^a	17.7 ^a	240 ^a	63.2 ^a	0.24 ^a	2.40 ^a
Quadrennial	6.30 ^a	1.77 ^{bc}	0.20 ^a	9.8 ^b	510 ^b	63.0 ^a	0.51 ^a	5.10 ^{bc}
Sexennial	6.32 ^a	1.66 ^b	0.20 ^a	10.5 ^a	320 ^a	63.2 ^a	0.32 ^a	3.20 ^{ab}
4-6 cm								
No burn	6.39 ^a	1.34 ^a	0.21 ^a	9.3 ^b	310 ^a	63.9 ^a	0.21 ^a	3.10 ^b
Annual	6.46 ^b	1.44 ^a	0.23 ^a	9.4 ^b	350 ^a	64.6 ^b	0.23 ^a	3.50 ^b
Biennial	6.40 ^a	1.62 ^b	0.14 ^a	11.8 ^a	520 ^b	63.7 ^a	0.14 ^a	5.20 ^{bc}
Triennial	6.47 ^b	1.48 ^b	0.09 ^a	17.1 ^a	305 ^a	64.7 ^b	0.09 ^a	3.05 ^{bc}
Quadrennial	6.42 ^a	1.33 ^a	0.09 ^a	19.6 ^a	225 ^a	64.2 ^a	0.08 ^a	2.25 ^a
Sexennial	6.34 ^a	1.34 ^a	0.08 ^a	19.1 ^a	290 ^a	63.4 ^a	0.08 ^a	2.90 ^a
6-8 cm								
No burn	6.43 ^a	0.99 ^a	0.08 ^a	14.9 ^a	265 ^a	64.3 ^a	0.08 ^a	2.65 ^{ab}
Annual	6.45 ^b	1.34 ^a	0.06 ^a	21.9 ^a	240 ^a	64.5 ^b	0.06 ^a	2.40 ^a
Biennial	6.44 ^b	1.47 ^b	0.07 ^a	21.0 ^a	460 ^b	64.4 ^b	0.07 ^a	5.60 ^c
Triennial	6.56 ^b	1.54 ^b	0.08 ^a	15.6 ^a	295 ^a	65.6 ^b	0.08 ^a	2.95 ^b
Quadrennial	6.56 ^b	1.24 ^a	0.09 ^a	13.6 ^a	300 ^a	65.6 ^b	0.09 ^a	3.00 ^b
Sexennial	6.47 ^b	1.20 ^a	0.08 ^a	16.0 ^a	255 ^a	64.7 ^b	0.08 ^a	2.55 ^a

Soil pH was not significantly correlated with total C, Ca, P, Na and the C:N ratio, but exhibited significant negative correlation with nitrogen and highly significant positive correlation with potassium concentrations (Table 4.5). There was no significant correlation between soil pH and fire frequency ($r = 0.34$; $P > 0.05$).

Table 4. 5 Correlation coefficients (r) for the relationship between soil pH and nutrient concentrations. (* Significant $P \leq 0.05$; ** Highly significant $P \leq 0.01$).

Soil nutrient	Correlation coefficient (r)
Total C	-0.25
Total N	-0.67*
C:N ratio	0.46
Ca	0.12
K	0.99**
P	0.12
Na	0.12

4.3.3 Treatment effects on N mineralization

Fire frequency significantly reduced N mineralization ($P \leq 0.05$; $n = 83$). Nitrogen mineralization was generally low across the treatments, with a range of between 4.8 and 9.6 mg/kg of soil. The annual burn resulted in a 42 % decrease in N mineralization, while the biennial burn resulted in the lowest decrease of 45 % compared to the no burn treatment (Figure 4.2). All the treatment means for the burnt plots were significantly lower than that of the no burn treatment ($P \leq 0.05$), but did not significantly differ from each other. There was a negative correlation between fire frequency and N mineralization ($r = -0.74$; $P \leq 0.05$). N mineralization had no significant correlation with either total N ($r = -0.38$; $P > 0.05$), total C ($r = 0.19$; $P > 0.05$) or the C :N ratio ($r = -0.41$; $P > 0.05$).

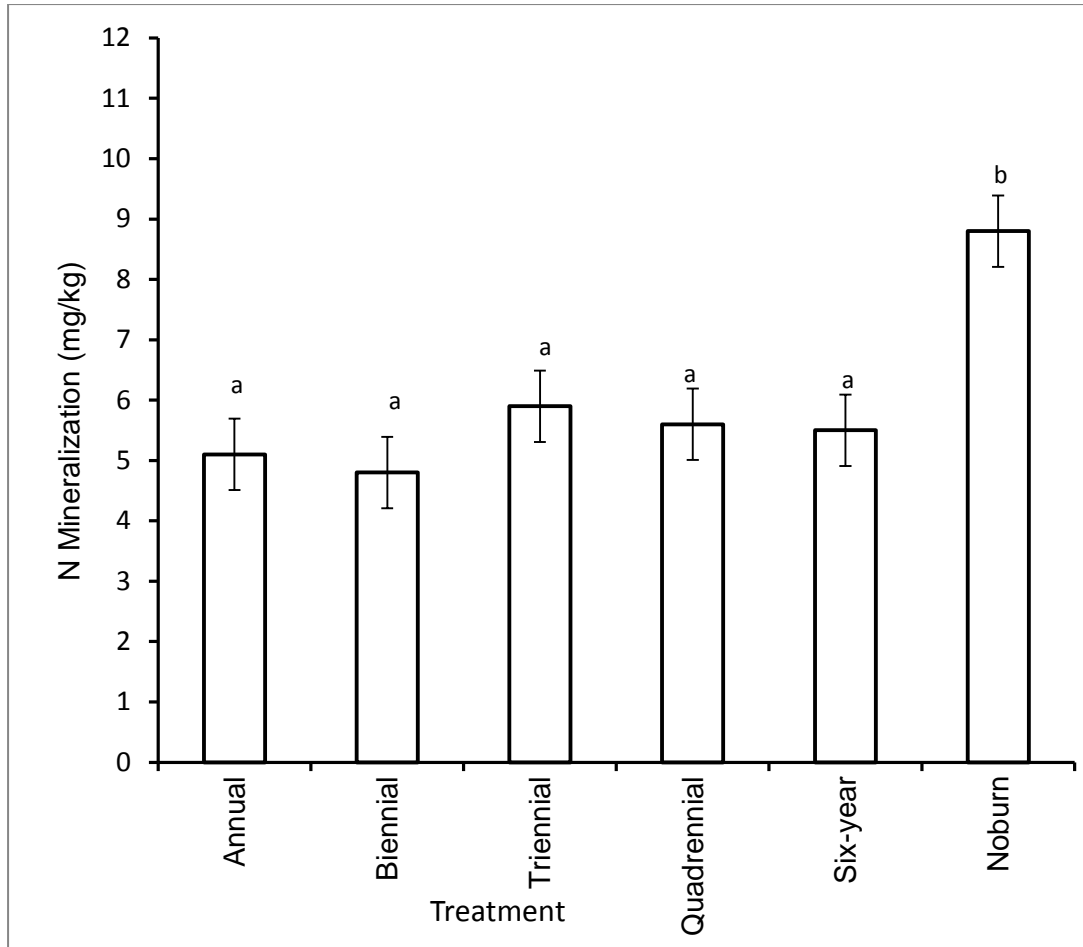


Figure 4.2 Mean (\pm SED) mineralized N concentrations of soils from a long-term fire trial at Fort Hare research farm. Means marked with the same letter are not significantly different ($P > 0.05$).

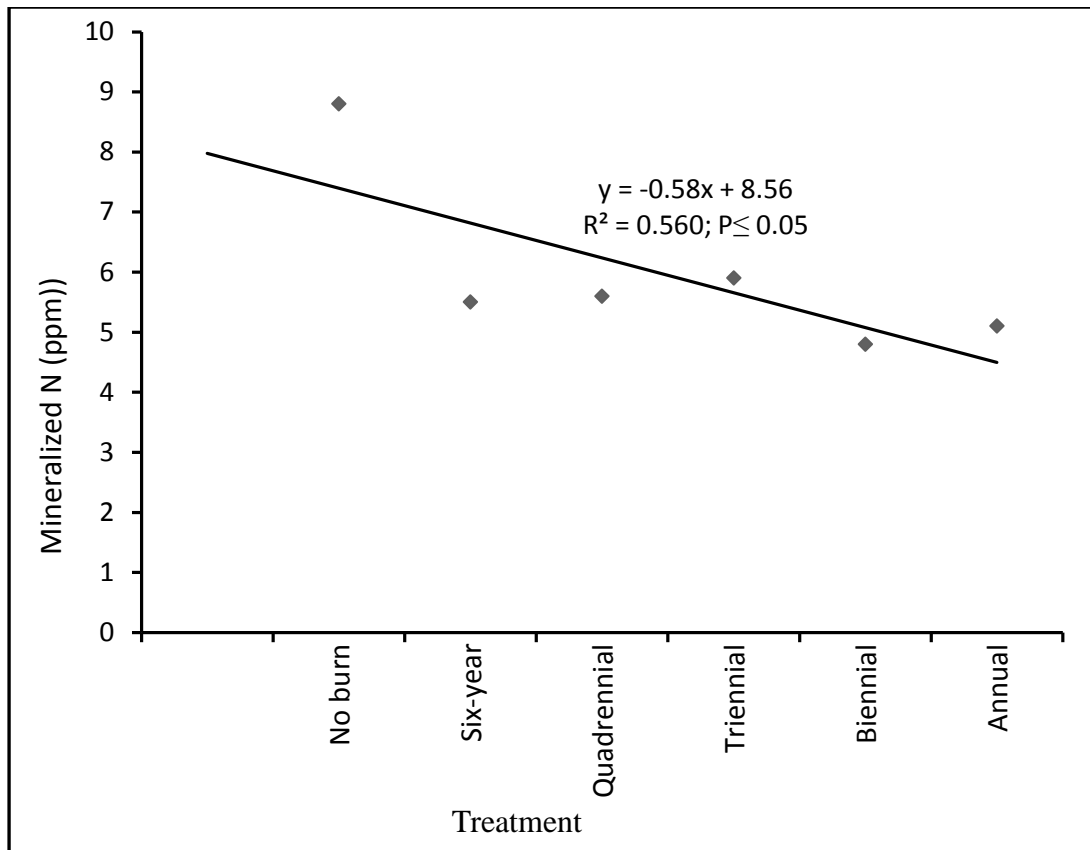


Figure 4. 3 Changes in N mineralization with different burning frequencies in a long-term trial at Fort Hare research farm.

4.3 Discussion

4.3.1 Treatment effects on soil pH

Nutrient elements in biomass and detritus experience one of three fates following a fire: They may be lost to the atmosphere, deposited as ash or remain in vegetation or detritus due to incomplete combustion (Boerner 1982). Ash, and to a smaller extent charcoal, remaining from biomass combustion retains large nutrient pools, and also produces a liming effect on surface soil (van Reuler and Janssen 1996; Glaser et al. 2002; Kurth et al. 2006). Despite the lack of significant treatment effect, the trends are comparable with similar studies. Materechera (et al. 1998) reported that frequently burnt plots produced significantly higher pH values than unburnt plots in the top surface soil (0-10 cm) from the same experiment twelve years earlier. Although the sampling depths are not identical in these two reports, similar trends could be expected. The results of this study (Table 4.2) follow a similar pattern, denoting the effectiveness of ash as a liming material on surface soil even the long term. These results are supported by Hogberg (1986) who highlighted that the liberation of base cations during fires in savannas causes a transient increase in soil pH. Soil pH and other factors such as temperature, soil moisture and aeration also influence litter decomposition and hence N mineralization (Scholes et al. 2003).

In this study, mean pH ranged between 6.29 and 6.42 which increased with fire frequency down the soil profile (Table 4.3), while it ranged between 5.53 and 5.77 and also increased with depth in the earlier study by Materechera (et al. 1998). A similar trend was also reported for a study conducted on a South African montane grassland by Manson (et al. 2007). The higher pH values in the longer-term results highlight the residual effects of fire on soil properties where fire is an ecological factor. According to Alberta Agriculture, Food and Rural Development (1998), the pH range in the study is conducive for nutrient solubility, especially the macronutrients. However, one should not undermine the complexity of ecological systems when evaluating fire effects because other confounding factors such as leaching, volatilization and the amount of biomass available for combustion may influence the results. For example, Mills and Fey (2003) found out that annual burn decreased soil

pH in some experiments, but increased it in others in similar conditions.

4.3.2 Effects on nutrient concentrations

Through burning, nutrients which accumulated in the plant biomass get released to some extent, and become partially available to plants which grow immediately after a fire (Boerner 1982; Roder et al. 1993). Studies have also indicated that yields of crops which grew after biomass burning declined during the following seasons or years (van Reuler and Janssen, 1993b; MacDicken and Ballard 1996). Consistent with other findings (Schacht et al. 1996; Materechera et al. 1998; Fynn et al. 2003), total C and N decreased with long-term burning frequency and also with soil depth. The most profound difference was in the uppermost layer (0-2 cm), and occurred between the annual and no burn treatments (Table 4.3), and it is likely that organic matter was the main source of these nutrients. A possible explanation for this trend would be that frequent burning reduces plant litter, and standing biomass, leaving less organic material available for combustion and incorporation of released nutrients into the soil profile. Burning generally reduces total N due to volatilization and mineralization (Schacht et al. 1996; Fynn et al. 2003; Snyman 2003), with most frequent burning treatments retaining organic matter with a lower N content than the organic matter retained in the no burn treatments (Manson et al. 2007).

Some studies have also reported no immediate response of total N (Nimir and Payne 1978) and total C (Manson et al. 2007) to burning. In this study, the N concentrations in the 0-2 cm layer were lower than in the 2-4 and 4-6 cm depths, which was making it more challenging to infer the trends of the results. The N concentrations for this trial were comparatively low (ranging from 60 to 230 kgN /ha) as compared to the 182 to 300kgN/ha for N pools for South African ecological systems, and 3 060 to 4 635 for southern African savannas. (Scholes et al. 2003). These results therefore imply the strong likelihood that N may be a limiting factor to productivity in this semi arid savanna. A possible explanation would be the high volatilization and accelerated use of soil N by microorganisms and higher plant life-forms following a fire. On the other hand, the soil is supposedly low in nitrogen even in areas where fire was not applied. A dairy farm was established adjacent to the long-term experiment in 2007, and the

farm manager (pers. com.) confirms the soil N and other mineral deficiency and the high input costs of improving soil fertility on the farm. The basic cations were positively influenced by burning frequency, and this was consistent with the findings of Materechera (et al. 1998) and Manson (et al. 2007). However, the mineral concentrations of the study conducted twelve years earlier by Materechera (et al. 1998) for the top soil (0-5 cm) were much higher than those presented in this study. These results entail that frequent burning could be beneficial by improving soil chemistry in the short and medium term, but may yield less positive results in the long term due to reduced plant biomass. Although the minimum and maximum C:N ratios ranged between 9.4 and 43, the mean C:N ratios ranged between 12 and 18 (Tables 4.2; 4.3), implying favourable conditions for N mineralization.

Where fire is common (hereby represented by frequently burnt plots), vegetation is a mosaic of patches of differing post-fire age (Forman and Boerner 1981), and the ash remaining may be distributed either horizontally to neighbouring sites by wind or surface erosion, or downward through leaching. In this study, just like in the earlier study by Materechera (et al. 1998), potassium was positively correlated with pH ($r = 0.58$) though the correlation is much stronger in these results ($r = 0.99$), highlighting the pH dependency of this nutrient. On the other hand, K increased while other basic cations (Ca and Na) increased down the soil profile, which was a direct opposite of the earlier results from Materechera (et al. 1998). A possible explanation would either be a loss due to the aforementioned horizontal redistribution of ash, or most probably due to reduced organic matter hence less nutrients available for release during combustion.

Climatic conditions, especially the timing of rainfall following a fire, also influences the fate of these nutrients. During the year of sampling, burning treatments were applied in late August, and it was possible for surface erosion to have washed away some of the ash by the time the resin bags were buried and soil samples collected. However, the higher K and N concentrations in deeper soils may be an indication that ash does not contain significantly higher concentrations of these nutrients. The lack of significant differences in most of the treatment means also imply that a 2 cm difference in sampling depth is not always a sufficient environmental gradient, hence

the differences are not large enough to quantify differences in soil chemical properties and nutrient distribution in soils.

4.3.3 Fire effects on N Mineralization

Disturbance usually increases nutrient availability and /or loss, with the amount of increase proportional to the degree of disturbance and nutrient status of the soil (Vitousek et al. 1987; Gillian 1988). In this study fire frequency significantly decreased nitrogen mineralization, with more frequently burnt plots (annual and biennial burns) resulting in the lowest nitrogen mineralization (Figures 4.2; 4.3). Similar results of reductions in soil mineralizable nitrogen under long-term fire regimes have been reported in North American grasslands (Turner et al. 1997; Blair 1997) and a South African mesic grassland (Fynn et al. 2003). The marked decrease in both total nitrogen and mineralizable nitrogen caused by long-term burning regime indicates a potential deficiency of nitrogen, which could ultimately result in low leaf protein content in plants growing on burnt areas, especially where burning is frequent and the rainfall is erratic and highly variable.

Rangelands generally have low protein content due to nitrogen limitation, and the main reason for the use of fire in grassland and savanna rangelands is the high protein content of post-fire re-growth. According to the results of this study, it appears that burning does not provide a long-term solution to this problem, but may essentially aggravate it. Inorganic nitrogen availability is also influenced by other environmental factors such as leaching of nitrate or its denitrification into deeper soil profiles, and insufficient water which could prevent nitrogen mineralization entirely (Vitousek et al. 1987). In this area of highly variable rainfall, drought is likely to be an important factor influencing soil nitrogen pools, especially where fire is involved. Although burning produces heat which can increase mineralization, it also dries out the soil and if there is insufficient rainfall following a fire, this could ultimately hinder mineralization. In fact, during the year of this study (2007), the annual rainfall was 506 mm while 742 mm was recorded in 2006. This high rainfall variability could influence post-fire nitrogen mineralization. Another factor would be the amount of nitrogen lost through volatilization during combustion.

The poor negative correlation between total N and mineralized N were similar to those obtained by Aarreira and Niell (1992) in a burned Mediterranean shrubland. However, the significant negative correlation between fire frequency and nitrogen mineralization indicates the significance of fire in influencing nitrogen cycling, but does not necessarily support the notion that periodic burning could play a significant role as a mineralizing agent of post-fire organic matter as suggested by Rice (1993). This lack of consistency in results obtained from different studies also demonstrates the fact that the effects of fire are generally confounded by other environmental factors because fire does not act in isolation. There is also a significant variation within and between different ecological systems in their responses to fire and other forms of disturbance.

4.3 Conclusions

It is important to quantify the effect of fire frequency on soil properties so as to understand its impact on soils and the environment, as it is commonly used as a management tool in agricultural and conservation systems. This study indicated some considerable variations in concentrations of essential nutrients, even though the variations were not large enough to explain the overall effects. Although a commonly recommended low-cost method of sustaining the vigour and productivity of warm-season grasslands (Schacht et al. 1996), this study has shown that fire also contributes to the cycling and redistribution of nutrients normally bound in aboveground biomass into the soil layers. This implies that timing and frequency of burn should be well managed to control nutrient distribution and maintain a sustainable balance in soil nutrient pools.

The fact that frequent burning reduced total carbon and nitrogen, hence narrowing the C:N ratio calls for caution and quantitative measures of loss due to volatilization as it affects nutrient pools. The significant decrease in nitrogen mineralization in frequently burnt plots also indicated that regular burning caused nitrogen loss and a greater nitrogen limitation in this semi-arid savanna in the long-term. Despite numerous reports of temporary post-fire increase in nitrogen availability, repeated burning especially in semi arid and steep areas may lead to a substantial depletion of the total nitrogen reserves in the system as evidenced by results of this study. Some older reports from the California chaparral also supported this observation by stating that more nitrogen was lost through volatilization and ash convection than remained in the ash (e.g Christensen and Muller 1973; Debano and Conrad 1978).

In this South African semi-arid savanna, fire is also widely used to control bush encroachment which reduces grass cover, and the bushes that are being reduced include leguminous trees such as *Acacia karroo*. These woody plants could contribute considerable nitrogen and organic matter which is reduced by burning, but their recruitment and phytomass is also greatly reduced by fire. The results highlight the negative impacts of high fire frequency and the complexity of managing arid and semi arid areas that are used for grazing. One can therefore deduce that fire has both

positive and negative long-term impacts on soils and vegetation. These findings necessitate careful consideration of nutrient dynamics in the soil-plant system where regular burning is administered with the intent to improve the protein content of post-fire vegetation in grazed ecosystems. It is therefore recommended that considerable accumulation of organic matter be allowed for the long-term sustainability of sound nutrient pools in South African fire-managed rangelands.

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CHAPTER 5 INVESTIGATION OF THE SHADE TOLERANCES OF SEVEN GRASS SPECIES FROM A SEMI-ARID SAVANNA

Abstract

The shade tolerances of seven perennial grass species from a South African savanna was investigated by subjecting them to different levels of shading for one growing season, and their biomass production compared on a dry matter basis. The species selected were: *Cymbopogon plurinodis*, *Digitaria eriantha*, *Eragrostis curvula*, *Melica decumbens*, *Panicum maximum*, *Sporobolus fimbriatus* and *Themeda triandra*. Seedlings of the seven grasses were propagated from cuttings collected from an upland area with fairly uniform soils in the False Thornveld of the Eastern Cape. In a split-plot design with six replications, one plant from each of the species was planted on a 22 cm plant pot and subjected to various shading intensities using dark shade netting. Treatments included full sun (0 % shading), 55 % shading, 70 % shading, 85 % shading and 93 % shading respectively. All plants were harvested, oven-dried and weighed to constant mass at 60 °C.

Digitaria eriantha produced a significantly higher overall biomass ($P \leq 0.05$), but experienced the sharpest decline in biomass with increase in shading intensity, followed by *Eragrostis curvula*, while *Melica decumbens* produced the lowest biomass, but was least affected by shading. The biomasses for *Cymbopogon plurinodis*, *Panicum maximum*, *Sporobolus fimbriatus* and *Themeda triandra* did not significantly differ from each other. From this study *D. eriantha* and *E. Curvula* are classified as shade intolerant, while *M. decumbens* is classified as shade tolerant. *C. plurinodis*, *P. maximum*, *S. fimbriatus* and *Themeda triandra* are classified as moderately shade-tolerant. The implication for sustainable range management is that appropriate gap size for satisfactory natural regeneration and seedling growth of savanna or open grassland species would therefore require a gap large enough to provide at least 30 % of ambient light.

Keywords: Biomass production, grass species, savanna grassland, shade tolerance.

5.1 Introduction

Light is one of the most studied ecological factors due to its importance to autotrophic life. It is not only light quantity that affects plant performance, but its quality and variability affect plant growth (Humbert et al. 2007). Many plants experience reduced solar radiation either from cloud cover or shading from their neighbours (Eriksen and Whitney 1982), and this invariably affects their energy capture. Variation in shade tolerance is a key factor underlying succession in many plant ecological systems such as forests (Skillman and Winter 1997; Kersteins 1999; Mason et al. 2004), grasslands and savannas (Wong et al. 1985b). Physiological ecologists believe that all else being equal, natural selection would favour plants whose form and physiology maximizes their rate of net energy gain (Bjorkman 1981; Givnish 1988). However, some degree of complexity may occur where a trade-off between energy capture and susceptibility to herbivores or other sources of mortality, and hence plant survival will not be determined by carbon balance alone (Kitajima 1994). Shade tolerance is therefore a fundamental plant attribute that is associated with a host of different traits, including aspects of carbon and nitrogen allocation to different functions such as photosynthesis, water and nutrient uptake and defence (Wong et al. 1985a; Kersteins 1998). It is therefore important to consider the possibility of other confounding factors when relating shade to various plant attributes.

The theory of shade tolerance suggests that there are species-specific physiological and morphological adaptations which influence their ability to survive and grow at different levels of light (Mason et al. 2004). There is no standard definition for shade tolerance, but it can be agronomically defined as the relative growth performance of plants in shade as compared to those in full sun as influenced by regular defoliation (Wong et al. 1985a). It embodies both dry matter production and plant persistence. Shade affects the persistence, growth, morphological and physiological development of plants as well as their leaf chemistry. Tiller production, leaf, stem, stubble and root production are often reduced at low light with the formation of thinner leaves with higher water content and a higher specific leaf area (Wong and Wilson 1980; Wong et al. 1985a). These morphological alterations are a result of resource allocation whereby increased dry matter production is prioritized towards shoot/leaf production at the expense of roots (Wong 1985a; Walters 1996).

5.1.1 Species classification based on shade tolerance

Though controversial, the classification of the shade tolerance of a species is generally based on the traits of a seedling, for it is generally agreed that the shade tolerance of a species differs little through ontogeny (Abrams and Mostoller, 1995; Poorter 1999; Kneeshaw et al. 2006). Species classified as shade tolerant should be able to germinate, grow and survive under low light environments, while the shade intolerant species require high light environments to germinate and grow (Walters 1996; Poorter 1999; Singhakumara et al. 2003). The shade tolerance of a species is often related to its successional status: Pioneer species which inhabit an area following a disturbance are usually classified as shade intolerant, while those dominating late succession seres are classified as shade tolerant (Walters 1996; Walters and Reich 1998; Landhausser and Lieffers 2001). The strategy of a shade tolerant species, commonly referred to as the 'sit and wait' strategy, is to stop or slow down growth in low light by reducing respiration (Messier and Nikinmaa 2000).

Shade tolerant species have developed some strategies to deal with low levels of light in various environments. These species are generally characterized by high light-induced morphological plasticity, slow relative growth rate, greater horizontal as opposed to vertical growth, extensive foliar display and low leaf mass per area (LMA) (Joesting et al. 2009). In tropical rainforests, with shade tolerant understory species, some measures that have been used to infer shade tolerance include high leaf area per unit leaf mass; low shoot to root ratio and smaller leaf mass per unit area (DeLucia et al. 1998; Singhakumara et al. 2003). Physiologically, shade tolerant species tend to have low photosynthetic rates, respiration rates; light compensation points (LCPs) and nitrogen content (Poorter 1999; Dalling et al. 2001). These plants also allocate most of their photosynthates to leaves to maximize light interception (DeLucia et al. 1998).

Species classified as shade intolerant need high irradiance regimes for establishment and growth. These plants generally germinate and grow quickly to attain canopy structure (Joesting et al. 2008). Shade intolerant species are also generally characterized by high photosynthetic and respiration rates, as well as high light compensation points and nitrogen content (Poorter 1999; Abram and Mostoller, 1995; Poorter 1999; Kneeshaw et al. 2006). These plants also generally have low light-

induced morphological plasticity, high relative growth rates, rapid vertical growth rates and high leaf mass per area (Poorter 1999; Dalling et al. 2001; Joesting et al. 2009). Some studies have indicated that tree species are able to alter their response to shade with ontogenic stage, such as species classified as moderately shade tolerant (Kloeppel et al. 1993; Naidu and DeLucia 1998).

5.1.2 Effect of shade on species' dry matter production

Shade imposes a limitation to primary productivity, although the limitation varies with shade tolerance of the species as well as nitrogen supply (Wong et al. 1985a). In a study conducted by Eriksen and Whitney (1985), grass yield increased linearly with increasing light up to 75 % of full sun, and then tended to plateau as light transmission increased to 100 % of full sun in high yielding grasses (e.g. *Panicum maximum*) supplied with nitrogen. An unusual effect of shade on grass yield was reported by Wilson (et al.1990) where the dry matter of *Paspalum notatum* was higher under *Eucalyptus grandis* shade than in full sun. This was attributed to the possibility that shade may have had a positive effect on the availability of soil nitrogen.

5.1.3 Impact of shading on rangeland dynamics

Degradation in the form of compositional change and reduced vegetation cover is a cause for concern to farmers and range managers as well as conservationists worldwide. This often leads to a need for restoration measures to be engaged to curtail the situation (e.g. improved forage production for livestock). In restoration of a species, Joesting (et al. 2009) and Pierson (et al. 2007) highlighted the importance of creating an optimum strategy of reintroduction due to high cost of seeds and labour required for restoration. This calls for deeper understanding of certain ecological concepts such as realized niche space, succession, recruitment limitation (e.g. shade tolerance), growth strategies and ecosystem function for successful restoration of a species. Weed invasion is also a general concern in range management, and especially in restoration of degraded rangelands. Therefore selection of re-introduced species should be done based on these concepts. For instance, Wong (et al. 1985) stated that an important character in the selection of shade-tolerant species is their ability to compete with shade-tolerant weeds under continual defoliation or herbivory.

There is limited information on persistence and dry matter production of pastorally and ecologically important species of the False Thornveld of the Eastern Cape, South Africa. A large proportion of this area is unsuitable for cropping, so the land is mostly used for livestock and game farming (Lent et al. 2000). In an effort to understand species performance with respect to shade tolerance, a study was undertaken to investigate the performance of seven native South African common grasses grown in pots under shading treatments that provided different levels of shade.

5.1.4 Objectives and hypothesis

The objective of this study was to investigate how common grass species differ in shade tolerance and to contribute to the understanding of how shade affects the performances of some selected common species of this semi-arid savanna. The results will provide some insight on how shade affects species composition and contribute towards developing appropriate grazing management to enhance the performance of pastorally important species.

The null hypothesis of no differences in the shade tolerances of the test species was tested.

5.2 Material and methods

5.2.1 Experimental setup

Seven perennial grass species were selected from a South African savanna for this experiment. The species selected were: *Cymbopogon plurinodis* Stapf. ex Burt Davy; *Digitaria eriantha* Steud.; *Eragrostis curvula* (Schrad.) Nees; *Melica decumbens* Thunb.; *Panicum maximum* (Jacq.); *Sporobolus fimbriatus* (Trin.) Nees and *Themeda triandra* Forssk. All seven species are dominants of southern African mid to late successional savanna communities. Except for *C. plurinodis* and *M. decumbens*, the other five species are readily grazed by livestock and game. *D. eriantha*, *E. curvula* and *P. maximum* are also widely used as cultivated pastures for grazing, hay or silage (Tainton 2000). The species' traits are presented in Table 5.1.

Table 5.1 Description of characteristics of the grass species used in the shade tolerance experiment.

Species	Growth form	Leaf blade anatomy	Shade tolerance	Succession status
<i>Cymbopogon plurinodis</i>	Tufted	C ₄	Moderate-high	Late
<i>Digitaria eriantha</i>	Tufted/ Stoloniferous	C ₄	Moderate	Intermediate
<i>Eragrostis curvula</i>	Tufted	C ₄	Low	Early
<i>Melica decumbens</i>	Tufted	C ₃	High	Late
<i>Panicum maximum</i>	Tufted	C ₄	Moderate	Intermediate
<i>Sporobolus fimbriatus</i>	Tufted/ Rhizomatous	C ₄	Low	Early
<i>Themeda triandra</i>	Tufted	C ₄	Moderate-low	Intermediate

*References: (Aranibar et al. 2008; Burton 1993; Gibbs-Russell et al. 1990; Grassroots 2004; O'Connor 1985; Ogle 2003; Steenekamp and Bosch 1995; van Oudtshoorn 1999; Veenendaal et al. 1996).

Single tillers of the seven grasses were propagated from cuttings collected from an upland area with fairly uniform soils in the South African semi arid savanna classified as the False Thornveld of the Eastern Cape (Acocks 1975). In a completely

randomized block design with six replications, one plant from each of the species was planted in a 22 cm plant pot and subjected to various shading intensities using dark shade netting. Species was used as a whole plot factor while shading intensity became the sub-plot factor. The shade treatments included full sun (0 % shading), 55 % shading, 70 % shading, 85 % shading and 93 % shading respectively. Dry mass per tuft was determined by harvesting, oven-drying oven-dried and weighed to constant mass at 60 °C. The experiment was run outdoors at the Neil Tainton Arboretum, University of KwaZulu-Natal facilities in Pietermaritzburg, and arranged as shown in Plate 5.1.

5.2.2 Statistical analysis

The effects of shade treatments and type of species on biomass production were tested using a 2-way ANOVA variance test. The analyses tested the dry mass for differences among species, among shading treatments and their interactions. Differences between arithmetic means for each species across the treatments were studied using Least Square Difference test. Multiple regression analyses were also conducted to test if there was a linear relationship between species and % shade. Prior to analyses the distribution of dry mass was examined for normality. Based on the results, the grass species were then classified as shade tolerant, moderately shade tolerant or shade intolerant.



Plate 5. 1 Layout of the shade tolerance experiment at Neil Tainton Arboretum, University of KwaZulu-Natal.

5.3 Results

Variance ratios of dry mass for the 2-way ANOVA showed significant differences between species, among the different shading treatments as well as the interactions between species and shade treatments ($P \leq 0.05$; Table 5.2). The results of the Analysis of Variance are presented in Table 5.2.

Table 5. 2 Variance ratios for the 2-way ANOVA on dry biomass of seven South African grass species grown under five shade treatments (0, 55, 70, 85 and 93 % shade). (n = 210; $P \leq 0.05$).

Factor	df	MS Effect	F	P
Species	6	181.09	24.14	< 0.000
Shade	4	188.54	25.13	< 0.000
Species x Shade	24	13.37	1.87	0.019

5.3.1 Species biomass production

Digitaria eriantha produced the highest overall mean biomass for all treatments, while *Melica decumbens* produced the lowest. The mean total dry mass for *Cymbopogon plurinodis* and *Eragrostis curvula* were significantly lower than those of *D. eriantha* but higher than those of the other four species ($P \leq 0.05$). The mean masses for *Panicum maximum*, *Sporobolus fimbriatus* and *Themeda triandra* did not significantly differ from each other, but were significantly higher than that of *M. decumbens* (Figure 5.1).

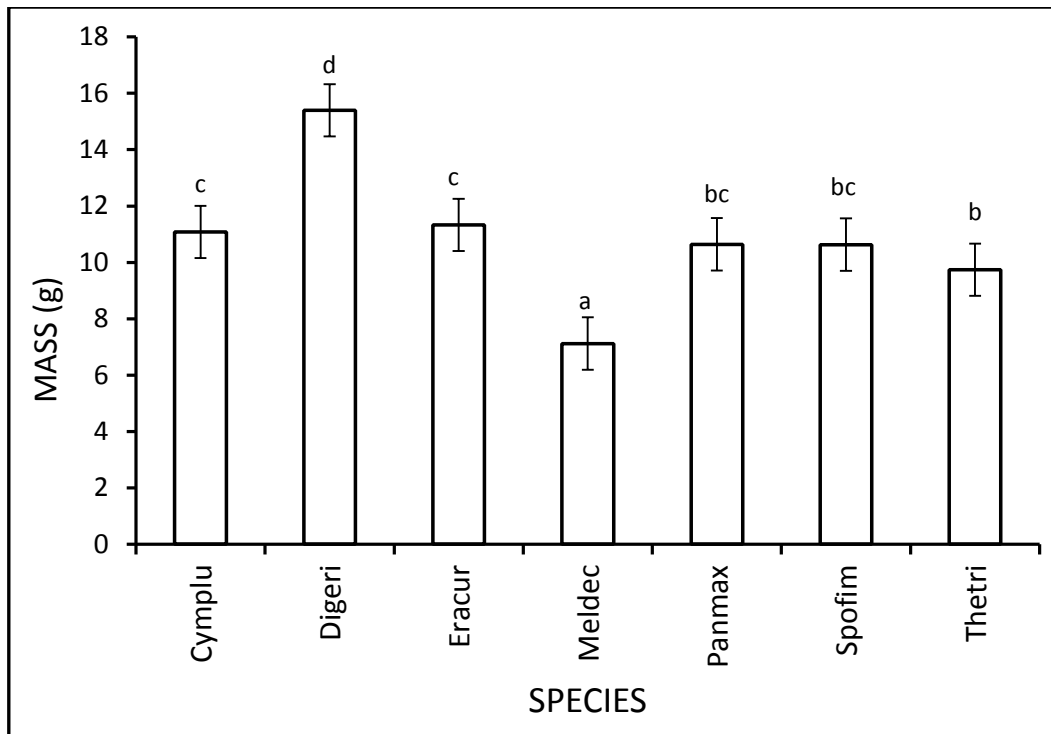


Figure 5. 1 Plot of overall means (\pm SE) for the dry masses per tuft of the seven grass species used in a shade experiment. Means with different letters are significantly different ($P \leq 0.05$).

KEY:(Cymplu: *Cymbopogon plurinodis*; Digeri: *Digitaria eriantha*; Eracur: *Eragrostis curvula*; Meldec: *Melica decumbens*; Panmax: *Panicum maximum*; Spofim: *Sporobolus fimbriatus*; Themtri: *Themeda triandra*).

5.3.2 Species' responses to shading

Trends among species were consistent across the shade treatments: The dry masses for all species generally decreased to varying magnitudes with increase in percentage shading (Table 5.3). Most of the species exhibited the highest mass increment under full sunlight (0 % shade), except for *Digitaria eriantha* which exhibited the highest significant biomass under the 55 % shade treatment. The lowest biomass was exhibited under 93 % shade for all the species and these means did not significantly differ from each other (Table 5.3). The dry mass of *Melica decumbens* was not significantly affected by shading, though it exhibited trends similar to the other species. Compared to the other grasses, *M. decumbens* experienced the lowest drop in biomass (14 %) between full sunlight and 93 % shade, compared with *D. eriantha* (58 %), *E. curvula* (51 %); *C. plurinodis* (46 %); *S. fimbriatus* (42 %); *T. triandra* (37%) and *P. maximum* (31 %) respectively.

Table 5. 3 Mean (\pm SE) dry mass per tuft (g) of grass each species grown under different levels of shading ($P \leq 0.05$).

Species	Percentage shade				
	0	55	70	85	93
<i>Cymbopogon plurinodis</i>	13.3(0.37) ^{bc}	13.1(0.22) ^b	11.8(0.11) ^b	10.5(0.14) ^b	7.2(0.57) ^a
<i>Digitaria eriantha</i>	17.0(0.11) ^c	21.2(4.09) ^d	14.8(0.98) ^{bc}	15.0(0.18) ^c	8.8(4.18) ^a
<i>Eragrostis curvula</i>	13.9(0.78) ^b	13.9(0.85) ^b	12.0(0.23) ^b	10.1(0.69) ^{ab}	6.8(1.18) ^a
<i>Melica decumbens</i>	7.6(1.25) ^a	7.3(1.59) ^a	7.0(0.52) ^a	7.1(0.55) ^a	6.5(2.81) ^a
<i>Panicum maximum</i>	12.3(0.04) ^b	10.3(2.05) ^b	11.2(0.13) ^b	10.8(0.71) ^b	8.5(1.25) ^a
<i>Sporobolus fimbriatus</i>	12.8(0.42) ^b	11.5(0.83) ^b	11.3(0.26) ^b	10.1(0.03) ^b	7.4(0.12) ^a
<i>Themeda triandra</i>	11.3(0.17) ^b	10.8(0.70) ^b	11.0(0.77) ^b	8.6(0.65) ^a	7.1(0.75) ^a

*Means with different letters in the same row and column are different ($P \leq 0.05$).

5.2.3 Relationships between species' biomasses and shade level

The results of the regression analyses indicated a linear relationship between the species dry masses and percentage shade ($P \leq 0.05$). The dry masses of all the grasses decreased linearly with an increase in percentage shade to various degrees (Table 5.3). The strongest linear relationship between dry mass and percentage shade was exhibited by *Digitaria eriantha*, while *Melica decumbens* exhibited the weakest linear relationship. Trends indicate that these two species were in opposite ends of the response hierarchy, while there was a closeness of responses (even an overlap) to shading between *Cymbopogon plurinodis*, *Eragrostis curvula*, *Panicum maximum*, *Sporobolus fimbriatus* and *Themeda triandra* (Figure 5.2).

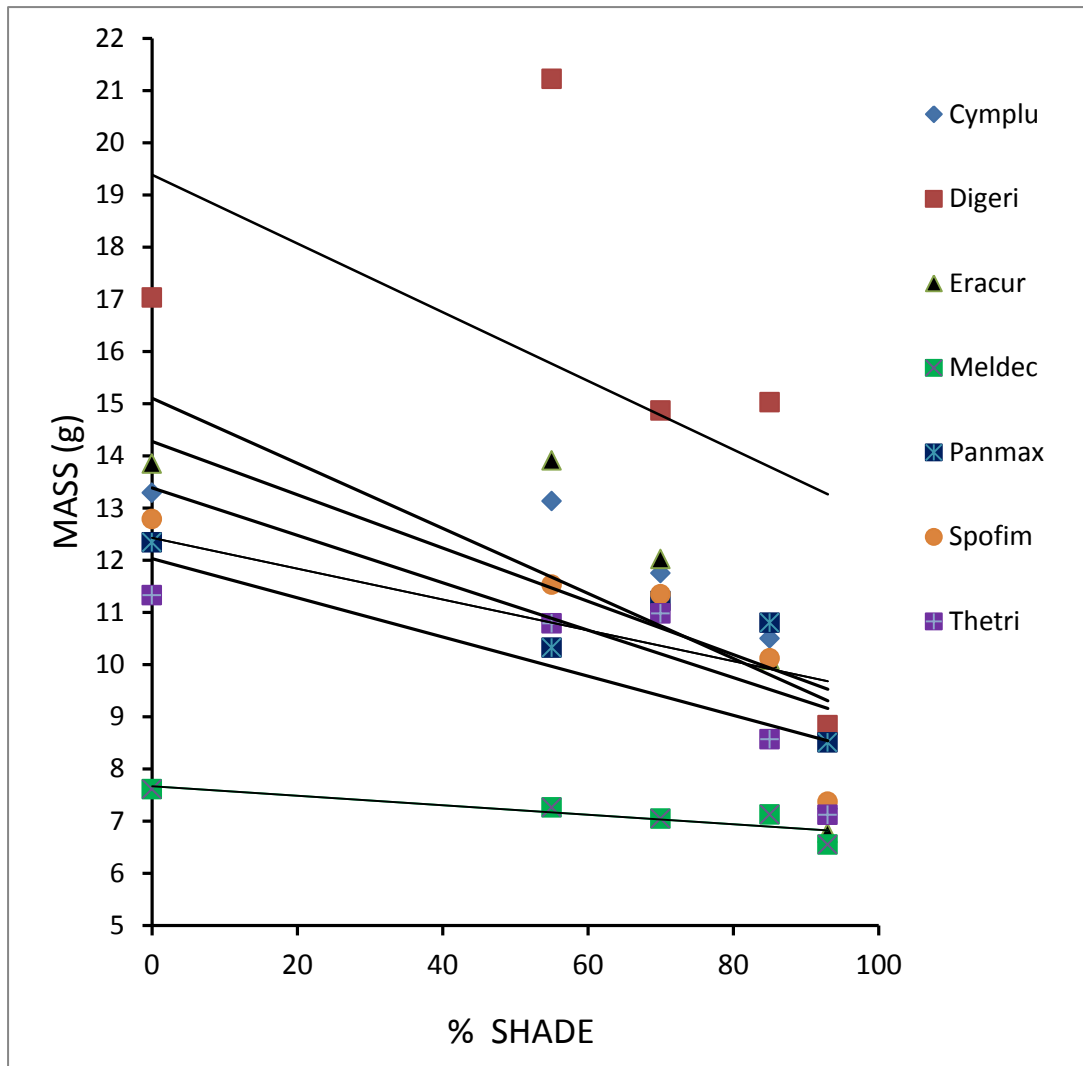


Figure 5.2 Regression plots indicating the changes in species mean biomass per tuft (g) with increase in shading level.

KEY:(Cymplu: *Cymbopogon plurinodis*; Digeri: *Digitaria eriantha*; Eracur: *Eragrostis curvula*; Meldec: *Melica decumbens*; Panmax: *Panicum maximum*; Spofim: *Sporobolus fimbriatus*; Themtri: *Themeda triandra*).

Table 5. 4 Regression results showing the relationship between species biomass and percentage shade for grass species six months after planting ($P \leq 0.05$).

Species	Equation	R²
<i>Cymbopogon plurinodis</i>	$y = - 0.051x + 14.27$	0.58
<i>Digitaria eriantha</i>	$y = - 0.056x + 19.38$	0.29
<i>Eragrostis curvula</i>	$y = - 0.062x + 15.10$	0.59
<i>Melica decumbens</i>	$y = -0.009x + 7.77$	0.76
<i>Panicum maximum</i>	$y = -0.029x + 12.43$	0.60
<i>Sporobolus fimbriatus</i>	$y = - 0.045x + 13.38$	0.67
<i>Themeda triandra</i>	$y = - 0.037x + 12.03$	0.57

5.4 Discussion

The results define the shade treatments under which the grass species attained their greatest and lowest biomass gain. Treatment effects on biomass accumulation indicate that all the species made their best growth performance in full sunlight (except for *Digitaria eriantha*). This closely follows the statement by Black (1957) that grasses generally make the fastest growth at or about full sunlight. The progressive decline in yield or dry mass from higher to lower light levels was also observed in other studies (e.g Tiedmann et al. 1971; Chen and Klinka, 1998; Mason et al. 2004). However, significant interaction between type of species and % shade indicate that the species responded differently towards shading. For instance, *Digitaria eriantha* exhibited a 20 % mass increase in 55 % shade over full sunlight, while *Cymbopogon plurinodis* and *Eragrostis curvula* yielded the same mean dry mass per tuft under full sunlight and 55 % shading respectively (Table 5.2). The between-species dry mass differences were more apparent under moderate to higher light conditions (0, 55 and 70 % shade), with *D. eriantha* and *C. plurinodis* showing greater responses to these conditions. Similar results were also obtained by Mason (et al. 2004) with *Pinus sylvestris* and *Picea sitchensis*. This type of response, according to Coates and Burton (1999), is a characteristic of shade intolerance.

Figure 5.2 indicates a decline in biomass production with increase in shading across all the species. *Eragrostis curvula* had the steepest slope, followed by *Digitaria eriantha* while that of *Melica decumbens* was the most gentle. These former two species are generally taller and hence produced the largest biomass per tuft under all shading conditions, while *M. decumbens* is naturally shorter than these two. However, the proportional differences between their biomass productions per tuft while growing under different shading conditions is indicative of their performances in response to shading. The trends indicate that *M. decumbens* did not experience significant reduction in biomass production while grown under shaded conditions compared to full sunlight. *Panicum maximum*, which often grows under tree canopies, exhibited a steady decline in biomass production with increase in % shade. Not surprisingly, it also did not have significant increase in biomass while growing in full sunlight compared to shaded conditions because it naturally thrives under partial shade. This is an advantage in terms of moisture loss.

5.4.1 Species classification based on shade tolerance

Dry mass gain as a measure of performance suggests that *Melica decumbens* was the least affected by shading, while *Digitaria eriantha* and *Eragrostis curvula* were most affected. The strong linear relationship of between shade and biomass production by *M. decumbens* and the insignificant relationship by *D. eriantha* (Table 5.3.) also showed that the two species reacted differently to shading; with the former responding in a more steady and predictable pattern and the latter rather more unpredictable. The less predictable response of *D. eriantha* is attributed to the fact that the species produced a higher biomass per tuft in partial shade (55 %) than in full sunlight. So unlike the other six grass species, there was no linear relationship between dry mass production of *D. eriantha* and % shading. Based on these results; *M. Decumbens* is categorized as being shade tolerant. According to van Wyk and van Oudtshoorn (2004); and from personal observation, *M. decumbens* is a climax species that normally grows between rocks and in the shade of trees and shrubs, and this affirms the findings of this study. This characteristic of growing in shade or on rocks may be a way of escaping heat in arid and semi-arid environments. This species is a short to medium grass classified as an Increase I (b) species (Trollope 1986), tends to disappear in disturbed areas. These features are in congruence with the statements that shade tolerant plants generally have a slow relative growth rate (Joesting et al. 2009), and dominate a late successional seres (Walters and Reich 1998; Landhausser and Lieffers 2001).

Digitaria eriantha was the most adversely affected by shading, hence is classified as shade intolerant. This characteristic of the species is also supported by the Natural Resources Conservation Service of the United States (2009); Gibbs-Russell (et. al. 1990) and Hacker (1992). Though shade intolerant, the results also showed that the species yields better in partial shade (± 50 %) than in full sun, a character that needs consideration for its use as a grazing or fodder crop. Van Wyk and Van Oudtshoorn (2004) also classified it as a climax species, while Trollope (1986) classified it as an Increaser II species (pioneer or low ecological status species). There is a general consensus that pioneer species are usually shade intolerant, while those dominating late succession seres are classified as shade tolerant (e.g. Walters 1996; Walters and Reich 1998; Landhausser and Lieffers 2001), and this agrees with the earlier

classification according to Trollope (1986) but in contrast with that of Van Wyk and Van Oudtshoorn (2004). However, Gibbs Russell (et. al. 1990) stated that the species is highly variable morphologically as well as in dry matter production, but this does not explain its dominance in climax vegetation when it is shade intolerant. In yet another study, Bosch and Theunissen (1992) found out that *D. eriantha* shifted its successional status with habitat type: In high rainfall areas it was classified as a Decreaser species (medium successional stage), but it reacted as an Increaser I species on the pediments of those areas. This would then agree with its classification by Van Wyk and Van Oudtshoorn (2004) as a climax species.

Panicum maximum, *Themeda triandra*, *Sporobolus fimbriatus* are classified as intermediate or moderately shade tolerant due to their close similarity in response to shade. *P. maximum* is extensively used as tropical forage and the results of work done in Malaysia (Wong and Wilson 1980; Wong et al. 1985b); Hawaii (Eriksen & Whitney 1982) and Australia (de Oliveira & Humphreys 1986) are in congruence with the ones obtained from this study with regards to the species being moderately shade tolerant. Though it grows well in damp areas under trees and shrubs and along rivers (van Wyk and van Oudtshoorn 2004), it is also found in open woodland and performs poorly under dense shade. de Oliveira and Humphreys (1986) indicated that dense shade also delays reproduction and also reduces seed production in *P. maximum*.

The classification of *T. triandra* as moderately shade tolerant is in harmony with its description by Australian National Botanical Gardens (2009) as a species that grows in full sun or partial shade. The species has been classified as a decreaser species, i.e. a species which is abundant in rangelands that are in good condition but decline when range deteriorates in condition (Bosch and Theunissen 1992; Steenekamp and Bosch 1996). Although *Sporobolus fimbriatus* often grows in damp places along rivers and next to roads, as well as in the shade (van Wyk and van Oudtshoorn 2004), and is in contrast classified as an Increaser II species by Trollope (1986), its response to shade was very similar to those of the other species classified as moderately shade tolerant.

Eragrostis curvula experienced a 51 % decline in dry mass (second highest to *Digitaria eriantha*), but its dry mass under full sunlight and at 93 % shade did not significantly differ from those of *Cymbopogon plurinodis* and the four species earlier classified as moderately shade tolerant. The lack of significant difference in the dry

masses of these five plants may be attributed to the fact that they are generally medium to tall species, so their overall yields may also be analogous as in Figure 5.1. *Eragrostis curvula* is therefore classified as moderately shade tolerant species, although it may to some extent exhibit some characteristics of a shade intolerant species. The plant is classified as a species of low ecological status (Steenekamp and Bosch 1996), and commonly grows in disturbed places such as overgrazed and trampled veld (Bosch and Theunissen 1992; van Wyk and van Oudtshoorn 2004).

According to the literature, *Cymbopogon plurinodis* is a climax species and has been classified as an Increaser I species, i.e. a species which is less abundant in veld that is in good condition, but increases when the vegetation is underutilized or selectively grazed (Trollope, 1986; van Rensburg and Bosch 1990). This is the same category as *Melica decumbens*, and is therefore anticipated to be shade tolerant. In this study however, it exhibited characteristics of a moderately shade tolerant to shade intolerant species since its dry mass did not significantly differ from those of *Panicum maximum*, *Themeda triandra* and *Sporobolus fimbriatus*, (Figure 5.2; Tables 5.2; 5.3). Veenendaal (et. al. 1996) and van Wyk and van Oudtshoorn (2004) reported that *C. plurinodis* grows in disturbed or undisturbed open grasslands alongside *T. triandra* or in open bush veld, and very seldom under tree canopy shade, and this may somehow explain the results of this study. Bosch and Theunissen (1992) found out that *C. plurinodis* is an Increaser I species in high rainfall areas but an Increaser II species in low rainfall areas. The reason it increases in low rainfall areas like the False Thornveld of the Eastern Cape is when the livestock ratio of sheep: cattle exceeds the recommended 3:1 and its increase in abundance is its response to being selectively not grazed. These contrasts also highlight the challenges of these types of classifications due to the effects of environmental variability and subsequent responses of these species to grazing.

5.4.2 Implications for range management

In this study, there is evidence suggesting that some of the grass species classified as either shade tolerant or intolerant are able to maintain higher levels of growth (hence biomass gain) while growing in partial shade as in full sunlight, or even better. The fact that some species that are good for grazing such as *Digitaria eriantha* can

perform optimally in partial shade can be advantageous in highly productive rangelands and pastures because when density is high, competition for light intensifies and shading can be a problem. In such conditions disturbance regimes such as fire and grazing (e.g. High Utilization Grazing) become important in providing appropriate gap sizes for efficient light penetration by removal of litter and removing top-hamper. In less productive areas, veld dominated by this species should preferably not be burnt to maintain the abundance of this species because burning will increase the availability of sunlight and therefore be disadvantageous to maintaining the abundance of this species. This calls for deeper understanding of light requirements of each species for optimum forage production rangelands.

The study also indicates that some species may alter their shade tolerance behaviour under certain environmental conditions, and this is in accord with the statement by Wong and Wilson (1980) that shade tolerance may be confounded with other factors such as growth habit and environmental stresses. It is also noticeable that classification of a species into any ecological group based on its shade tolerance or vice versa, is challenging. Shade tolerance does explain a significant amount of interspecific differences, but its use as a surrogate for classification into an ecological or successional status may, as indicated by Kersteins (2001), be complicated by the possibility of a combination of characteristic traits that allow the species to persist in shade. Therefore, shifts do occur depending on environmental conditions due to phenotypic plasticity exhibited by certain species, especially the intermediate or moderately shade tolerant species. The practical application of this study to range management in highly variable and complex environments such as savannas requires determining critical light levels for seedling survival and growth, and linking these to observations of light regimes in the field.

5.5 Conclusions

This study demonstrates the differential degrees of shade tolerance among common species of a semi arid savanna. In summary, it was clear that all the seven species can endure a certain degree of shading before being adversely affected. The results also showed that some grasses of open grasslands such as *Digitaria eriantha* can actually perform the same as, or even better in partial shade than in full sunlight. From this study *Digitaria eriantha* was adversely affected by shading, hence is classified as shade intolerant, while *Melica decumbent* is classified as shade tolerant. *Cymbopogon plurinodis*, *Eragrostis curvula*, *Panicum maximum*, *Sporobolus fimbriatus* and *Themeda triandra* are classified as moderately shade-tolerant. The hypotheses of no differences in the shade tolerances of the test species is therefore rejected.

It is also apparent that using yield or dry matter change as the sole variable for determining the shade tolerance of a species is inadequate in providing more meaningful results for range management application. The declining dry matter production with increasing shade levels necessitates proper range management to ensure high productivity and persistence of pastorally important grasses in a constantly changing light environment such as those characterized by strong seasonality. An implication for sustainable range management is that appropriate gap size for satisfactory natural regeneration and seedling growth of savanna or open grassland species would therefore require a gap large enough to provide at least 30 % of ambient light. This would entail either controlled burning where the grass has become moribund, and also controlling area and species selective grazing so that most of the grazing area is moderately grazed to reduce excessive shading.

For future studies, it is recommended that other morphological and physiological variables such as leaf size/area, root: shoot biomass, number of leaves/tillers, net photosynthetic rate, etc. need to be included in factorial experimentation for broader understanding of the mechanisms of survival and performance under shaded conditions.

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CHAPTER 6 COMPETITIVE EFFECTS AND RESPONSES OF SELECTED SPECIES IN A SOUTH AFRICAN SAVANNA

Abstract

The competitive effects and responses of seven perennial grasses and one woody plant commonly found in South African semiarid savanna were investigated in two competition experiments using the phytometer species technique. The species comprised *Cymbopogon plurinodis*, *Digitaria eriantha*, *Eragrostis curvula*, *Melica decumbens*, *Panicum maximum*, *Sporobolus fimbriatus*, *Themeda triandra* and *Acacia karroo*. The competitive responses of the species were determined in an outdoor split-plot factorial experiment at the University of Fort Hare research farm. Competition intensity was used as a whole-plot factor (no neighbour, 2 neighbours, 8 neighbours), while clipping and soil fertility were sub-plot factors each at two levels (clipping and no clipping; fertilizer and no fertilizer) respectively, with five replications. Seedlings of these plants were propagated in a glass house prior to commencement of the trial and transplanted onto 1m² plots. All aboveground material was harvested, oven-dried and weighed. Competitive response was determined using ANOVA for split-plot design on the natural log of the phytometer masses. Relative Interaction Indices were determined by comparing the species' dry mass of species while growing with neighbours to their dry mass without neighbours.

Competition intensity, soil fertility and clipping had significant effects on the biomass production of the phytometer species, while all interactions between these variables were not significant. Of the seven grasses, *P. maximum* and *D. eriantha* produced the highest biomasses across all the treatments, and *M. decumbens* produced the lowest. The Relative Interaction Indices (RRI's) of the phytometers varied significantly between the species, competition intensities and the interaction between fertility level and type of species significantly affected RRI's. Clipping and all other possible interactions did not have a significant effect on the RRI of the phytometer species. *C. plurinodis* exhibited the weakest competitive interaction (RRI = -0.19), followed by *E. curvula* (-0.29) and *M. decumbens* (-0.31), while *S. fimbriatus* had the strongest competitive interaction (-0.47) followed by *T. triandra* (-0.45), *D. eriantha* (-0.35)

and *P. maximum* (-0.34). *E. curvula* exhibited the strongest competitive effect, followed by *D. eriantha* and *P. maximum*, while the bottom three were *C. plurinodis*, *A. karroo* and *M. decumbens* respectively.

The study therefore supports the ‘resource pre-emption’ model, which states that larger plants usurp resources at the expense of smaller plants because of their ability to secure more than their proportional share of resources as based on their relative size.

Keywords: Competitive effect, competitive response, clipping, fertility, grass species, phytometer, Relative Interaction Index.

6.1 Introduction

Since the early twentieth century, nine basic interactions between individuals in an ecological community have been recognized. These include amensalism, commensalism, competition (direct interference type), competition (resource-use type), mutualism, neutralism, parasitism, predation and proto-cooperation (Clements et al. 1929; Burkholder 1952; Haskel 1949). Among these, resource-use-type competition has long been recognized as the ‘dominant law of relationships’ between individuals and species in plant communities (Tansley 1920). There is therefore a consensus that botanical composition and productivity of any vegetation is largely determined by competitive interactions (e.g. Newman 1983; Wilson 1988). Competitive interactions of a species may not only explain the relative abundance of a species in a given community, but may also provide some insight into the nature of forces that structure such a community (Miller and Werner 1987).

Competition is important in both natural and agricultural plant communities. Understanding how competition varies with productivity is thus vital for differentiating among models of plant community structure and function. Models that do not include mechanisms of interactions among organisms can describe the phenomenology of population interactions, but cannot predict the community dynamics or the outcome of these interactions (Tilman 1990). Therefore there is need to include environmental variables and mechanisms of interactions in efforts to develop predictive theories of competition and succession in different plant communities.

6.1.1 Concepts and theories of plant competition

The ability of a species to persist and prosper in a community is often determined by its competitive interactions with other species (Connell 1983). Competition generally implies exploitation of limited resources that are essential for their life, primarily light (above-ground), water and nutrients (below-ground). Because nutrients are heterogeneously distributed, the fate of a plant largely depends on its local environmental settings (Aerts 1999; Berger et al. 2008). Although root and shoot functions are fundamentally integrated (McPhee and Aarssen 2001), the spatial

division between them and the differences in the microclimate experienced by each has received considerable attention in recent efforts to understand the mechanisms of competition and the bases of differences in competitive abilities among species.

Three models or hypotheses are commonly used in plant ecology to predict changes in competition intensity with standing crop along principal natural gradients. The first model is that competition for both light and soil resources increases with productivity (Grime 1977; Chapin 1980; Keddy 1989). The second is that competition for light increases with standing crop but competition for belowground resources declines (Grubb 1985; Tilman 1988), and the third states that competition intensity is minimal in plant communities of low (but not the lowest) productivity (Oksanen 1993; Sammul et al. 2000). Experimental evidence supporting these models has been derived through work on both natural and experimental resource gradients that are characterized by turnover in species composition or life form (Peltzer et al. 1998). It is conceded that species in natural communities are organized into transitive competitive hierarchies, and that these hierarchies vary among environments (Keddy et al. 1994). Habitat fertility and disturbance are the two major variables that have been recognized as major underlying determinants of plant community organization (Grime 1977; Tilman 1988), while competition determines species distribution and abundance along fertility gradients (Grime 1979; Austin 1990). However, the influence of competition on extremely low and high fertility gradients is highly contentious (Fynn et al. 2005).

6.1.2 Competitive response and competitive effect

Most ecologists agree that competition is an important structuring factor in plant communities, but researchers disagree on the circumstances where it is most intense, and on which traits can be considered to contribute to competitive ability in different species. Competitive ability has two components: competitive effect and competitive response. The distinction between a species' effect on resources and its response to reduced resource levels might help to solve these questions. Competitive effect is defined as the ability to depress the growth or reproduction of neighbours; and competitive response as the ability to withstand the negative effects of neighbours (Goldberg 1990). These two components attempt to predict species interactions relative to resources, which are often in short supply. Competitive effect predicts how

an individual depletes resources, and therefore how it influences their amount available to other organisms, and how it performs and survives in response to depleted resources (Goldberg and Werner, 1983; Suding et al. 2004). Successful species must have either a low response to the abundance of other species, and/or a large enough effect that the abundance of other species is significantly reduced (Miller and Werner 1987). Therefore, a species may either have a low response and a high effect, or any other combination of effect and response.

Competition is a result of plant density and size relative to available resources (Zedaker 1982). Essential resources such as nitrogen and phosphorus can limit primary production of individual plants (Tilman 1982; Ingestad and Agren 1995), and can play a role in plant community assembly (Daufresne et al. 2005). Therefore understanding plant-herbivore, plant-plant and plant-nutrient interactions are challenges for plant community ecology and ecosystem biology. The process of competition is not measured directly. The presence and intensity of competition are inferred from stand and plant-level attributes measured within populations grown under different density and site conditions and how these attributes change over time. These density-induced effects are assumed to be the outcome of competition between individual plants.

Patterns of competitive effects and responses are particularly challenging in plant communities due to the heterogeneity of their natural habitats and resource availability. To address these challenges, competitive abilities of species can be determined experimentally by growing species in additive mixtures and measuring the reduction in their performances in mixtures relative to controls (Keddy et al. 1994; Sammul et al. 2000). Making such comparative measures is one of the several research strategies in plant ecology. In this study, eight species (seven grasses and one woody plant) were being explored and ranked relative to their competitive effects and responses in different environments.

6.1.3 Rationale and Objectives

In the False Thornveld of the Eastern Cape, most of the agricultural land is used for pastoral farming with cattle, sheep, goats, and to a lesser extent, game farming. One

of the problems facing farmers and range managers is compositional change whereby the more acceptable grass species are replaced by less desirable grasses or even trees and shrubs (primarily *Acacia karroo*).

This study is aimed at investigating competitive interactions between selected species in a simulated non-selective grazing environment across a soil fertility gradient.

The following key questions were asked:

- How does competition intensity affect performances of selected common species of the False Thornveld of the Eastern Cape?
- How do disturbance and soil fertility affect competitive effects and responses of these species?
- Do the interactions between these two variables influence competitive hierarchies of these species?

6.2 Material and Methods

6.2.1 Selection of species

The selection of species was aimed at selecting native grasses that are of some ecological or pastoral importance, and can hence be used as ecological indicators of rangeland condition. The eight species (from henceforth referred to as phytometer species), comprised seven native perennial grasses and a woody plant-*Acacia karoo*. The seven grass species are categorized as Decreaser species (*Panicum maximum* and *Themeda triandra*); Increaser I species (*Cymbopogon plurinodis* and *Melica decumbens*) and Increaser II species (*Digitaria eriantha* and *Eragrostis curvula*) based on their responses to grazing intensity in the False Thornveld of the Eastern Cape. Decreaser species are grasses of high grazing value, and their abundance is indicative of good veld, and these species decrease in poor rangeland that is overgrazed or selectively grazed (understocked). Increaser species have poor forage value, and increase with overgrazing (Increaser II species), or with understocking and selective grazing (Increaser I). The eighth phytometer species, *Acacia karoo* (Hayne), is a short to medium tree included because of its ecological importance in this vegetation type. The woody plant has encroached large areas of this semi-arid savanna vegetation, which is also classified as the False Thornveld of the Eastern Cape by Acocks (1988). *A. karoo* has significant competitive interactions with grasses, especially in areas with high grazing pressure. A summary of the grass species' traits is presented in Table 5.1 (Chapter 5). *Eragrostis curvula* was chosen as a universal neighbour due to its versatility and the fact that its seeds were available commercially.

Seedlings of *Acacia karoo* and the seedlings of *Eragrostis curvula* that were planted as neighbours were propagated through seed germination. *A. karoo* seeds were abundant in the natural vegetation while seeds for *E. curvula* were purchased from commercial seed suppliers. The rest of the 7 phytometer species were propagated vegetatively using cuttings of young shoots from the surrounding natural vegetation because their seeds were neither available commercially nor were they easily obtainable from the natural vegetation. All the seedlings were propagated individually

on seedling trays in late August 2005, five weeks prior to commencement of the experiments.

6.2.3 Competitive response experiment

The responses of the eight phytometers species to competition intensity under different levels of soil fertility and simulated non-selective grazing (clipping) were determined in a plot-based outdoor experiment. The site comprised an area of land that was previously cultivated at the University of Fort Hare research farm, but was abandoned five years earlier due to poor productivity. The site was ploughed in October 2005 to remove all existing vegetation and the soil was tilled to enable easier transplanting of seedling. An individual seedling from each of the eight phytometers was planted in the centre of a 1m x 1m plot, and neighbours of *Eragrostis curvula* were planted 15 cm around it. Low competition was simulated by two neighbours on opposite sides of the phytometer, while high competition was represented by eight neighbours planted equidistant around the phytometer. Control phytometers for each species were grown with no neighbours, no clipping either at high or low fertility level (LAN fertilizer or no fertilizer), and at two levels of simulated non-selective grazing (clipping and no clipping). The treatments are summarized in Table 6.1.

Table 6. 1 Description of treatments used in the competitive response trial

Factor	Levels	Description
Species	8	A-H
Soil fertility	2	No fertilizer, fertilizer
Clipping	2	No clipping, clipping
Competition	3	no neighbours, 2 neighbours, 8 neighbours

The experiment was conducted in a split – plot factorial design with five replications per treatment, where soil fertility was used as a whole plot factor, while competition intensity and clipping were used as sub-plot factors. The clipping was done once in January, which is usually the middle of the growing season. The plants were irrigated twice a week when it was dry and once a week under normal rainfall conditions so

that water did not become a limiting factor, and observations (and mortalities, if any) were made daily. In the first week of May 2006, all aboveground plant material was harvested by cutting all material 20 mm from ground level with grass sickles for both phytometers and neighbours. The material for each phytometer was placed in separate paper bags and oven-dried to constant mass at 60 °C and weighed. The experiment was allowed to run for a second consecutive year (i.e. until May 2007) to compare the results of the two growing seasons. Competitive response was measured as the extent to which overall growth was suppressed by neighbours (Wilson and Keddy 1986; Campbell and Grime 1992).

6.2.4 Competitive effect experiment

A pot experiment was conducted in pots placed under shade netting (90 % light penetration) to investigate the competitive hierarchies of the eight species described in Table 6.1. The eight species were each propagated in a glass house in August-September 2007. Transplants were then grown in pots containing 3000 cm³ of fine river sand from October 2007 till May 2008. The treatments included the 8 aforementioned phytometer species, all grown at three fertility levels i.e. 0 %, 50 % and 100 % Hoagland's solution (Wang et al. 2009), and two levels of simulated non-selective grazing (clipping, no clipping). Each of the eight species was used as a phytometer in mixed cultures, with or without four neighbours of *Eragrostis curvula* planted 7.5 cm around the phytometer. The experimental design allowed the comparison of growth and survivorship of each species when growing with or without neighbours. During the duration of the experiment, any weeds that grew in the pots other than the experimental transplants were removed on a daily basis. On the 10th of May 2008 the experiment was terminated by removing all plant material from the potting medium, and cutting off the roots so that only the masses for shoots from individual tufts were considered. The harvested tufts were placed in separate labelled paper bags, oven-dried to constant mass at 60 °C and weighed. The mean mass for each species was determined for each treatment. Roots were not included because root composition was not part of the study, but only shoot competition was investigated in the trial.



Plate 6.1a Arrangement of phytometer (centre) and eight competitors placed 30 cm around it in the outdoor plot experiment (September 2006).



Plate 6.1b Appearance of the competition trial just before harvest in April 2007.



Plate 6. 2 Layout of the pots at commencement of the trial (October 2007).

6.2.4 Data analyses

Competitive response was measured as the natural logarithm of the relative biomass of a species grown with competition compared to its mass when grown without competition. The Relative Interaction Index (Armas et al. 2004) for each species under different levels of competition, soil fertility and clipping was determined as follows:

$$Y = X_0 - X_1 \div X_0 + X_1$$

Where; Y= Relative Interaction Index

X_0 = species mass without competition

X_1 = species mass with competition

Competitive effect was determined by comparing the competitive ability (biomass) of each species while growing with *Eragrostis curvula* (interspecific competition), to its strength without competition at different levels of soil fertility and clipping. The phytometer mass was regressed against neighbour mass, yielding per-gram competition coefficients. The effects of treatments on the competitive abilities of the species were tested using a 3-way ANOVA, while all pairwise comparisons were tested using Tukey's test at 95 % confidence intervals. All the species experienced some mortality, but in all the treatment replications, there were individuals that survived to the end of the experiment. Since all treatments were replicated 5 times, the mortalities were treated as missing values. All data were analyzed using GenStat 11 for Microsoft Windows.

6.3 Results

6.3.1 Competitive responses

Competition intensity, soil fertility and clipping had significant effects ($P \leq 0.05$) on the biomass production of the phytometer species. Moreover, the competitive responses to these variables varied significantly among the different species ($P \leq 0.05$; Figure 6.1). All possible interactions between these variables were not significant ($P > 0.05$). (See Appendix 1 for the complete ANOVA output table). In general, as the density of neighbours increased, the growth of all phytometers was significantly reduced (Figure 6.1). *Acacia karroo* and *Melica decumbens* were so adversely affected by competition intensity that mortalities often occurred, especially when growing with eight competitors. *M. decumbens* was also very sensitive to clipping, such that many of its phytometers failed to re-grow after clipping, while soil fertility had a less important role in their performances. In total, 13 % of *Cymbopogon plurinodis*, 21 % of *A. karroo* and 35 % of *M. decumbens* phytometers died during the course of the experiment, and most of the mortalities occurred just after clipping. Other phytometer species experienced less than 5 % mortalities.

Clipping reduced the productivity of all the species, while fertilizer application enhanced it (Table 6.3). *Panicum maximum* and *Digitaria eriantha* produced the highest biomasses across all the treatments, while *A. karroo* and *M. decumbens* had the lowest biomasses in all the treatments. The rest of the other species ranged between these two extreme scenarios, with *C. plurinodis* ranging just above the bottom two, and *Eragrostis curvula* below the top two species (Table 6.3). Tukey's pairwise multiple comparison test indicated that mean (log) mass between most of the eight phytometer species were significantly different across the treatments ($P \leq 0.05$). The only non-significant interactions ($P \leq 0.05$) occurred between the *Cymbopogon plurinodis*-*Themeda triandra*, *Digitaria eriantha*-*Panicum maximum* and *Themeda triandra*-*Sporobolus fimbriatus* pairs. The results of all possible interactions relative to the Tukey test are presented in Appendix 3.

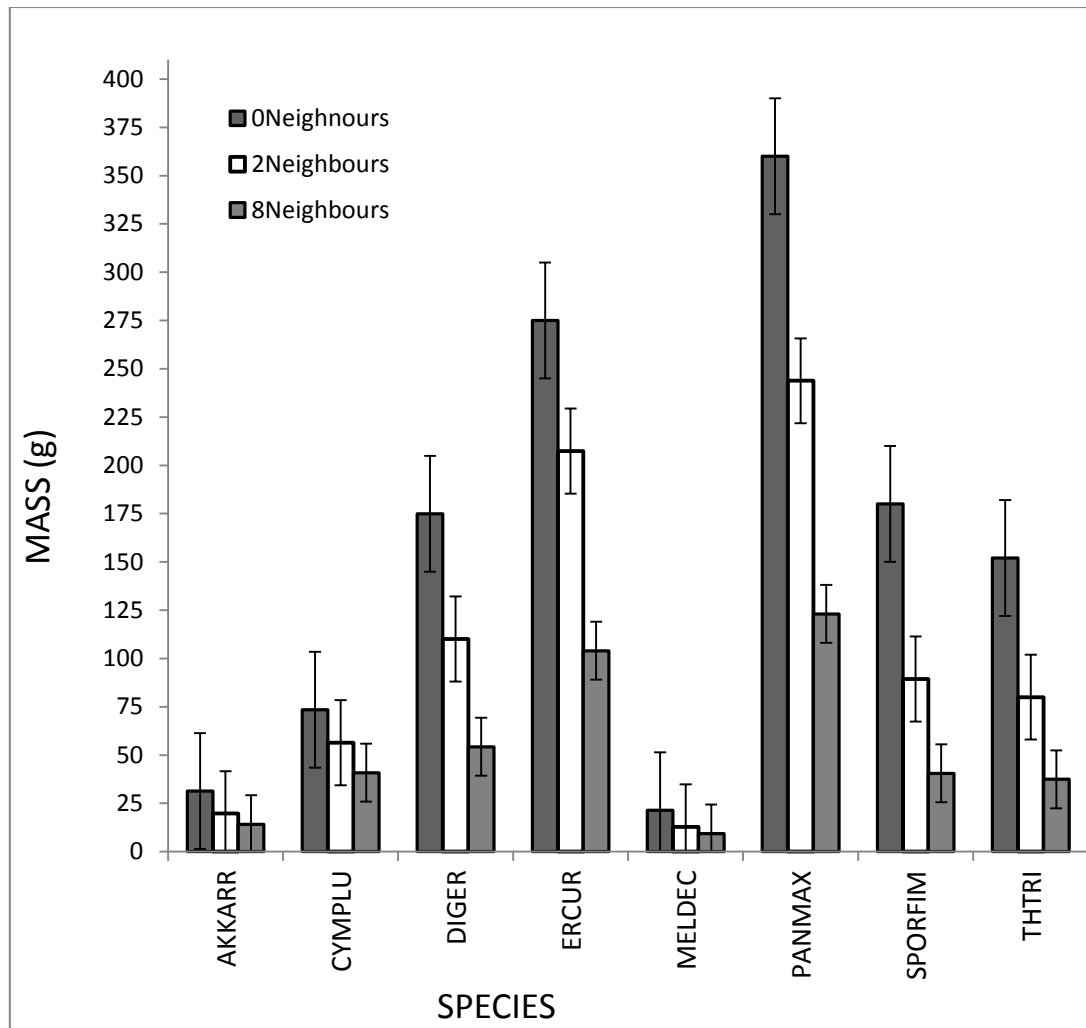


Figure 6. 1 Mean (\pm S.E.) for (log) mass of the eight phytometer species for the main effect of competition with 0, 2 and 8 neighbours respectively.

(KEY: AKKARR= *Acacia karroo*; CYMPLU = *Cymbopogon plurinodis*; DIGER= *Digitaria eriantha*; ERCUR = *Eragrostis curvula*; MELDEC = *Melica decumbens*; PANMAX = *Panicum maximum*; SPORFIM = *Sporobolus fimbriatus*; THTRI = *Themeda triandra*)

Table 6. 2 Mean (log) mass per tuft for the phytometer species at different levels of clipping and fertility. (n= 196; $P \leq 0.05$).

SPECIES	CLIPPING		FERTILITY	
	No Clip	Clip	No Fertilizer	Fertilizer
<i>Acacia karroo</i>	1.40 ^b	1.23 ^b	1.32 ^b	1.31 ^a
<i>Melica decumbens</i>	1.19 ^a	1.09 ^a	1.11 ^a	1.67 ^b
<i>Cymbopogon plurinodis</i>	1.80 ^c	1.69 ^c	1.75 ^c	1.73 ^b
<i>Themeda triandra</i>	1.93 ^d	1.84 ^d	1.85 ^d	1.94 ^c
<i>Sporobolus fimbriatus</i>	2.01 ^e	1.87 ^d	1.93 ^e	1.95 ^c
<i>Eragrostis curvula</i>	2.10 ^f	1.95 ^e	1.97 ^e	2.04 ^d
<i>Digitaria eriantha</i>	2.31 ^g	2.21 ^f	2.16 ^f	2.36 ^e
<i>Panicum maximum</i>	2.34 ^g	2.30 ^g	2.33 ^g	2.36 ^e

Means with the same letters along the same column are not different ($P > 0.05$).

6.3.2 Species Relative Interaction Indices

The Relative Interaction Indices (RRI's) of the phytometers varied significantly between the species ($P \leq 0.01$), competition intensities ($P \leq 0.01$) and the interaction between fertility level and type of species significantly affected RRI's ($P \leq 0.05$). Clipping, and all other possible interactions did not have significant effects on the RRI of the phytometer species ($P > 0.05$). (Appendix 3). The results for the overall mean RRI coefficients for the species are presented in Figure 6.2. The general trends are that *Cymbopogon plurinodis* exhibited the weakest competitive interaction (RRI = -0.19), followed by *Eragrostis curvula* (-0.29) and *Melica decumbens* (-0.31), while *S. fimbriatus* had the strongest competitive interaction (-0.47) followed by *Themeda triandra* (-0.45), *Digitaria eriantha* (-0.35) and *Panicum maximum* (-0.34). Interestingly, *Acacia karroo* exhibited a stronger competitive interaction than the three weakest grass species (Figure 6.2).

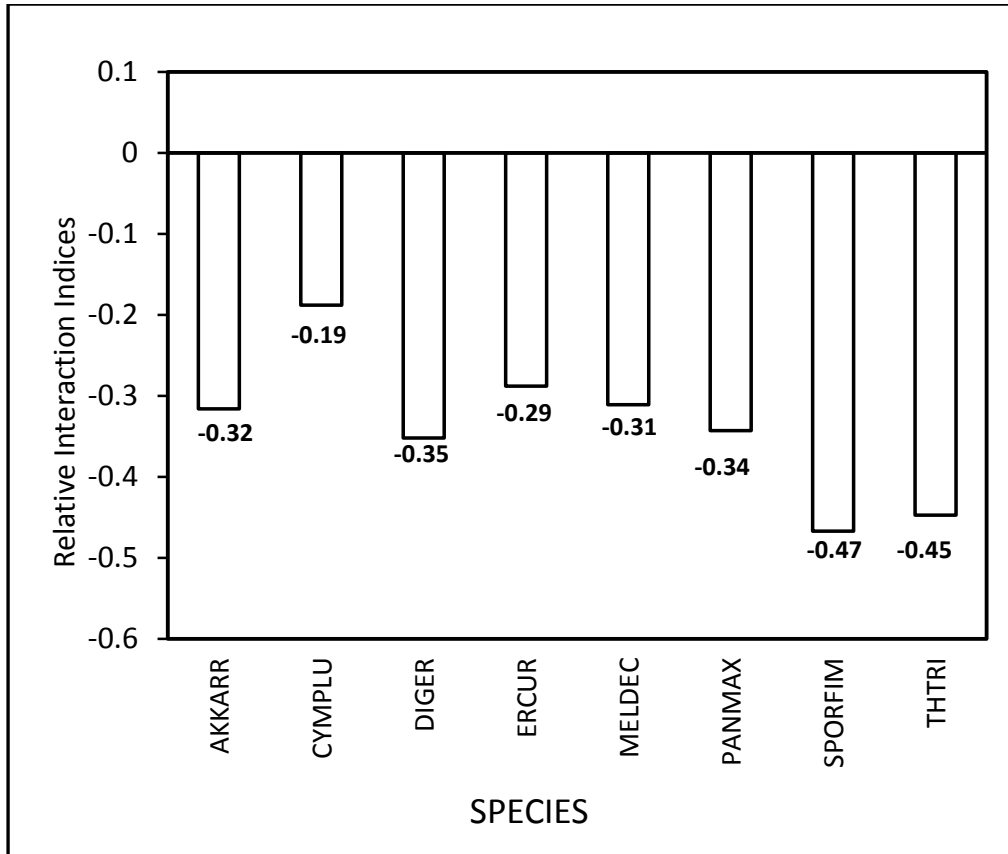


Figure 6. 2 Mean RII coefficients for phytometer species

(See Figure 6.1 for full species; names)

Relative competition intensity was generally higher at higher fertility levels, and for most of the species, it increased with the number of neighbours (Table 6.3). Although *Sporobolus fimbriatus* and *Themeda triandra* continued to show the strongest suppressive response to neighbours in all the treatments, some minor shifts in species' competitive hierarchies were observed between the two competition intensities and fertility levels. For instance, *Eragrostis curvula* had a stronger competitive interaction coefficient (-0.56) than *Digitaria eriantha* (-0.53) and *Panicum maximum* (-0.48) with two neighbours in the high fertility treatment (Table 6.3). Also, *Acacia karroo* exhibited the second strongest interaction in high fertility with eight neighbours (same as *S. fimbriatus*), while *T. triandra* exhibited the highest interaction index, indicating that it is being strongly suppressed by neighbours. Despite these aforementioned shifts, the trends in interaction rankings were consistent; with *S. fimbriatus* being the weakest competitor and *C. plurinodis* being the strongest competitor (Tables 6.2 and 6.3).

Table 6. 3 Mean Relative Interaction Indices of phytometer species for competition intensity between fertility levels (n= 268; $P \leq 0.05$).

COMPETITION INTENSITY	SPECIES	FERTILITY LEVEL	
		No fertilizer	Fertilizer
2 neighbours	<i>Acacia karroo</i>	-0.22 ^a	-0.26 ^a
	<i>Cymbopogon plurinodis</i>	-0.17 ^a	-0.18 ^a
	<i>Digitaria eriantha</i>	-0.29 ^{ab}	-0.53 ^b
	<i>Eragrostis curvula</i>	-0.20 ^a	-0.56 ^b
	<i>Melica decumbens</i>	-0.17 ^a	-0.31 ^a
	<i>Panicum maximum</i>	-0.27 ^{ab}	-0.48 ^b
	<i>Sporobolus fimbriatus</i>	-0.35 ^b	-0.69 ^{bc}
	<i>Themeda triandra</i>	-0.30 ^b	-0.61 ^b
8 neighbours	<i>Acacia karroo</i>	-0.24 ^{ab}	-0.55 ^a
	<i>Cymbopogon plurinodis</i>	-0.07 ^a	-0.33 ^b
	<i>Digitaria eriantha</i>	-0.15 ^{ab}	-0.49 ^{ab}
	<i>Eragrostis curvula</i>	-0.09 ^a	-0.30 ^b
	<i>Melica decumbens</i>	-0.34 ^b	-0.42 ^{ab}
	<i>Panicum maximum</i>	-0.14 ^a	-0.49 ^{ab}
	<i>Sporobolus fimbriatus</i>	-0.30 ^b	-0.55 ^a
	<i>Themeda triandra</i>	-0.30 ^b	-0.57 ^a

Means with different letters along the same column are different ($P \leq 0.05$).

6.3.3 Species' competitive effects

Clipping and fertility had significant effects on the biomass production of phytometers as well as neighbours ($P \leq 0.05$), and the mass of the various species were significantly different across the treatments ($P \leq 0.01$). There was significant interaction between fertility and clipping ($P \leq 0.05$), and these two factors significantly affected the biomass of the phytometers as well as neighbour plants ($P \leq 0.05$; Appendices 3 and 4). The general responses of both phytometers and neighbours to clipping were similar: biomass production for all plants increased with increase in fertility, while clipping greatly suppressed the plants (Figure 6.3). Of the eight phytometer species, *Digitaria eriantha* generally exhibited the strongest competitive

effect by having the highest growth (biomass production) and having the strongest suppressive effect on its neighbours, while *Melica decumbens* exhibited the weakest suppressive effect (Figure 6.4). *Themeda triandra* also showed a very weak ability to suppress neighbours, ranking only second lowest to *M. decumbens*.

6.3.4 Effects of clipping and soil fertility on species' performances

The species showed some shifts in competitive responses to clipping along fertility gradients: In poor or infertile soil (0%, no clipping), *Eragrostis curvula* exhibited the strongest competitive effect, followed by *Digitaria eriantha* and *Panicum maximum*, while the bottom three were *Cymbopogon plurinodis*, *Acacia karroo* and *Melica decumbens* respectively (Table 6.4). However, *D. eriantha* and *P. maximum* exhibited stronger competitive ability than *E. curvula* after clipping in the low fertility treatment. *Themeda triandra* also performed better after clipping than when unclipped in poor soil fertility. Under moderate fertility (50 %) with no clipping, *D. eriantha* performed slightly better than *E. curvula*, while the rest of the hierarchy remained the same. A dramatic shift in competitive ability occurred in the high fertility (100 %) treatment: *D. eriantha* still came on top when the plants were unclipped, but after clipping, *P. maximum* exhibited the strongest competitive response to clipping in high fertility treatment than all the other species, while *E. curvula* exhibited the weakest competitive ability (Table 6.4).

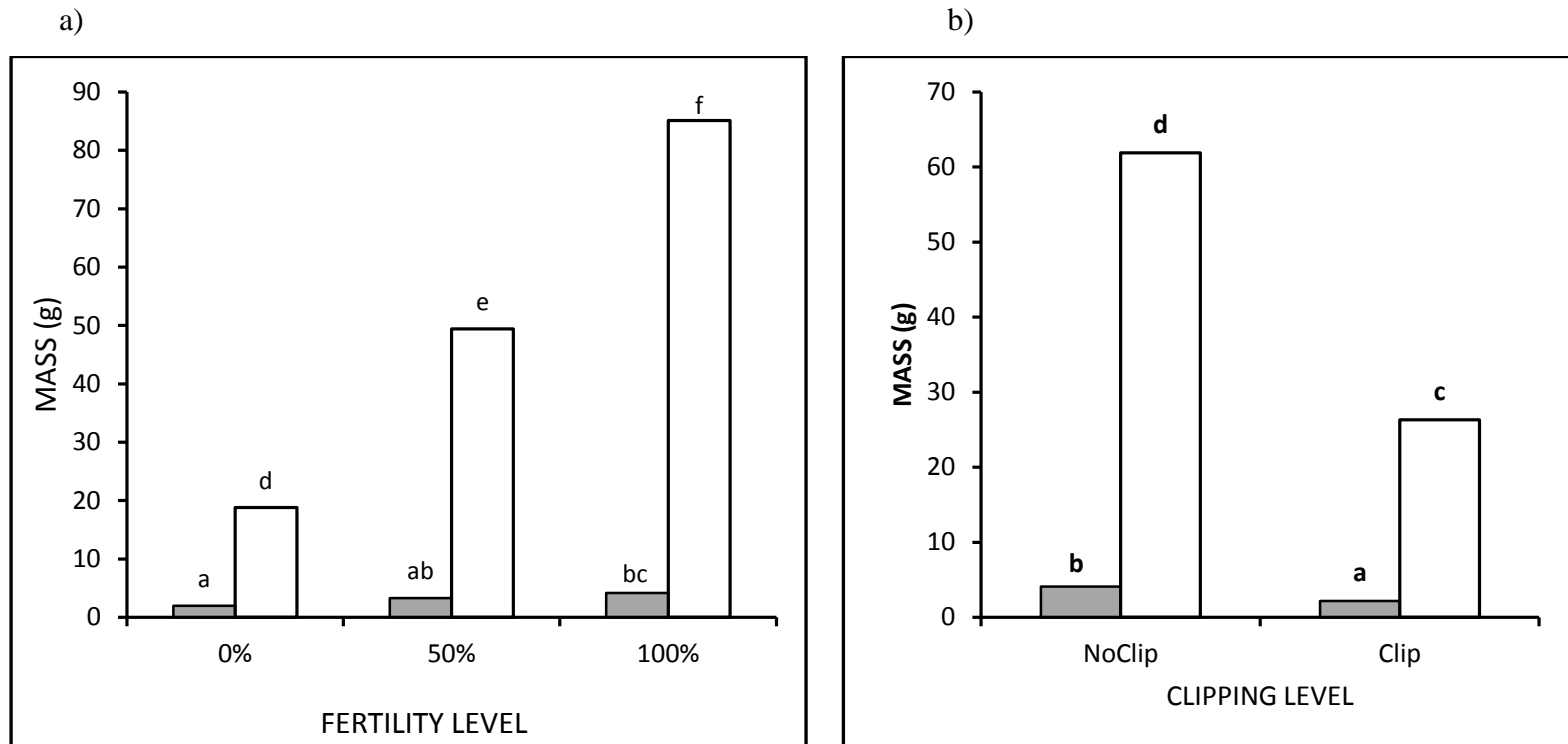


Figure 6. 3 Mean biomass per tuft for phytometers and neighbours for the main effects of a) fertility and b) clipping. Means for graphs with different letters are significantly different ($P \leq 0.05$).

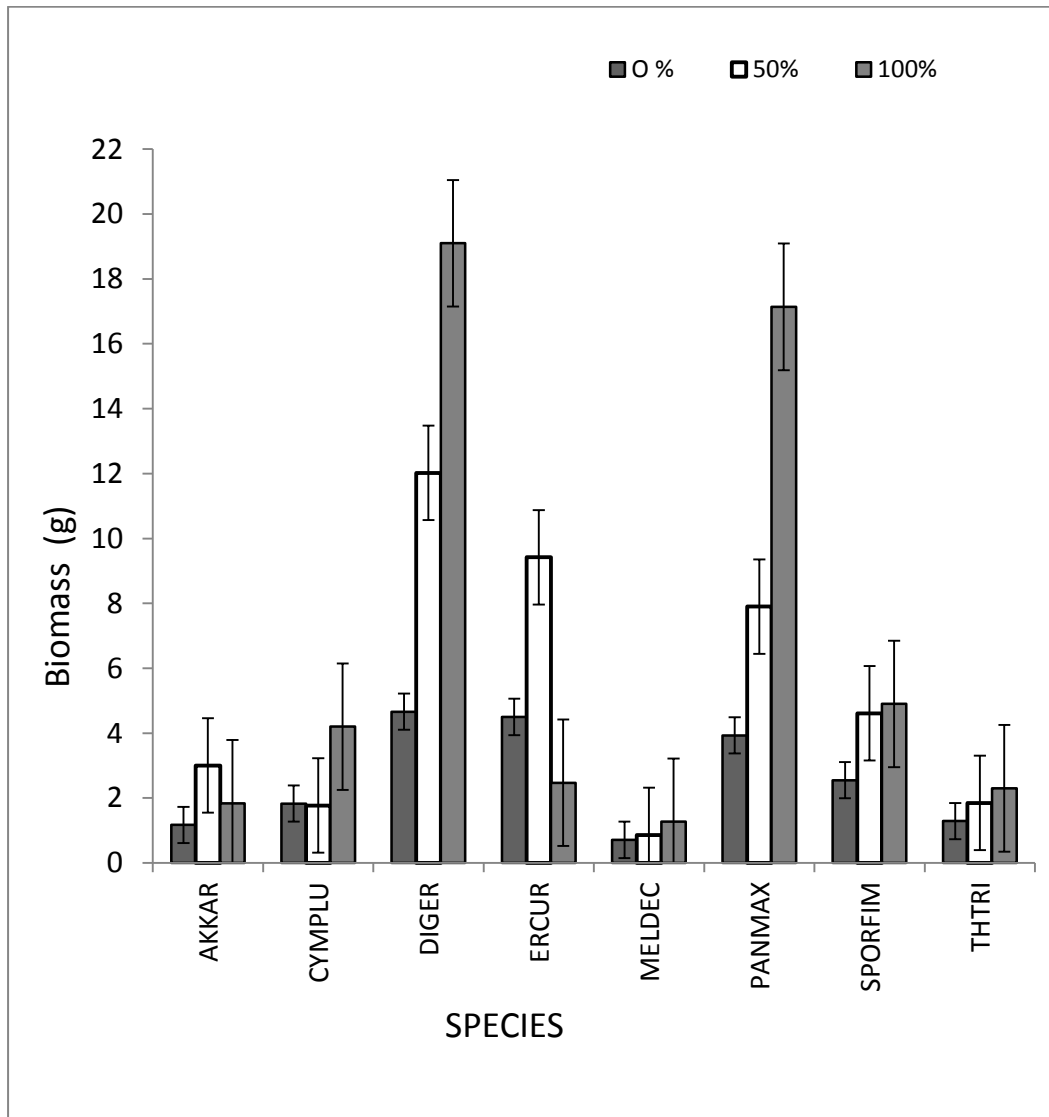


Figure 6. 4 Mean (\pm S.E.D.) biomass of all phytometers for the main effect of fertility in the pot trial.

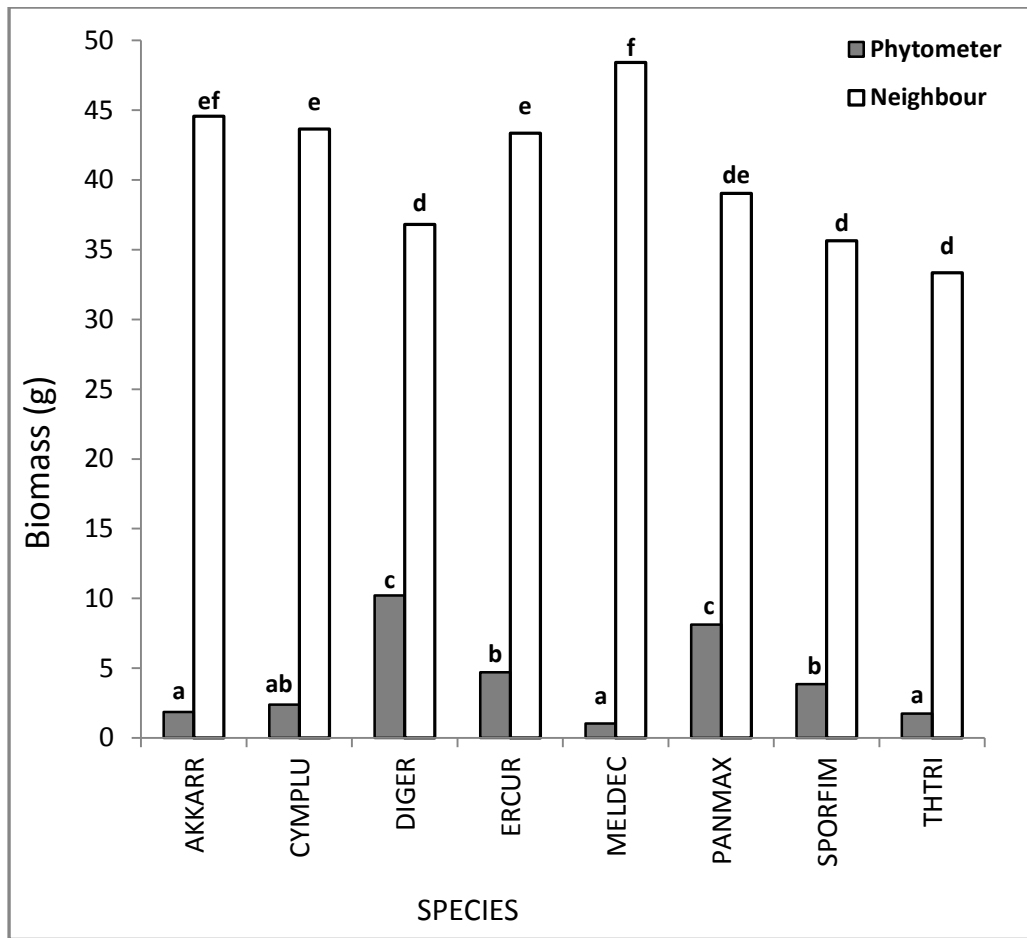


Figure 6. 5 Overall mean biomass of all phytometers and their neighbours for the pot trial. Means with different letters are significantly different ($P \leq 0.05$).

Table 6. 4 Mean (log) biomass of phytometer species for the interaction between clipping and fertility in the competitive effect trial (n=196; $P \leq 0.05$).

FERTILITY LEVEL (%)	SPECIES	CLIPPING	
		No Clipping	Clipping
0	<i>Acacia karroo</i>	0.42 ^b	-0.28 ^{ab}
	<i>Cymbopogon plurinodis</i>	0.52 ^b	0.00 ^b
	<i>Digitaria eriantha</i>	0.81 ^{bc}	0.52 ^{bc}
	<i>Eragrostis curvula</i>	1.07 ^c	0.24 ^{ab}
	<i>Melica decumbens</i>	-0.30 ^a	-0.52 ^a
	<i>Panicum maximum</i>	0.80 ^{bc}	0.39 ^{bc}
	<i>Sporobolus fimbriatus</i>	0.71 ^{bc}	0.10 ^{bc}
	<i>Themeda triandra</i>	0.03 ^b	0.19 ^{bc}
50	<i>Acacia karroo</i>	0.53 ^b	0.43 ^b
	<i>Cymbopogon plurinodis</i>	0.23 ^b	0.27 ^b
	<i>Digitaria eriantha</i>	1.28 ^c	0.88 ^c
	<i>Eragrostis curvula</i>	1.24 ^c	0.71 ^c
	<i>Melica decumbens</i>	-0.41 ^a	-0.47 ^a
	<i>Panicum maximum</i>	0.99 ^c	0.82 ^c
	<i>Sporobolus fimbriatus</i>	0.95 ^c	0.38 ^b
	<i>Themeda triandra</i>	0.44 ^b	0.09 ^b
100	<i>Acacia karroo</i>	0.09 ^a	0.44 ^a
	<i>Cymbopogon plurinodis</i>	0.46 ^a	0.79 ^{bc}
	<i>Digitaria eriantha</i>	1.41 ^c	1.15 ^c
	<i>Eragrostis curvula</i>	0.81 ^b	-0.02 ^a
	<i>Melica decumbens</i>	0.06 ^a	0.15 ^a
	<i>Panicum maximum</i>	1.22 ^c	1.25 ^c
	<i>Sporobolus fimbriatus</i>	0.74 ^b	0.64 ^b
	<i>Themeda triandra</i>	0.64 ^b	0.08 ^a

Means with the same letters along the same column for each fertility level are not significantly different at $P \leq 0.05$.

6.4 Discussion

6.4.1 Species' competitive effect and response hierarchies

Theory states that plants respond to density-induced stress (i.e. competition) through two negative feedback mechanisms: plasticity, by altering both the growth rate and the numbers of their component parts, and mortality, which occurs when the ability of a plant to compensate for competitive stress via plasticity is exceeded (Harper 1977; Grime et al. 1986). Supporting these theories were the findings of this study in which the growth or biomass production of all the eight test species was significantly reduced by increase in neighbour density to varying levels (Figure 6.1). Of the eight species, an invasive shrub, *Acacia karroo* and a C₃ grass species, *Melica decumbens*, exhibited the weakest competitive effects and responses: These two species produced comparatively low biomasses in all treatments, and also experienced the highest mortalities, signifying their poor ability to withstand intensive growth suppression by neighbours. Similar results were obtained by Keddy (et al. 2002) who reported that the weaker competitors in both control and stress treatments tended to be small grasses and sedges. On the other hand, two tall, broad-leaved species (*Digitaria eriantha* and *Panicum maximum*) and one tall, narrow-leaved species (*Eragrostis curvula*) exhibited the strongest competitive effects by producing significantly higher biomasses, having a noticeably higher suppressive effects on neighbours (Figure 6.5) and experiencing very low or no mortalities. The other species ranked between the aforementioned.

In view of these results, careful consideration should be made with respect to inequality in plant size and variation in growth rates of test species. In this study, *Melica decumbens* is a comparatively smaller tufted grass than the other six, hence its low biomass production was to be expected. Similarly, *Acacia karroo* also had a low biomass production, and this is not surprising because woody plants generally have a relatively lower growth rate compared to herbaceous species (Brand et al. 1987). However, the fact that all the test species coexist and hence interact in the same environment necessitated the need to investigate their competitive interactions because of their role in community structure and functioning. Inequality in plant size and variation in growth rate is a product of the interaction between genetic variability,

environmental heterogeneity and competition (Dyer 1997). In this study, the larger and faster-growing species performed better than the smaller, slower-growing species in terms of survival and biomass production.

These results appear on one hand, to support the conceptual model which suggests that competition acts on all individuals equally or in direct proportion to their size, commonly called the 'resource-depletion' model (Weiner 1985; Weiner and Thompson 1986). On the other hand, the fact that the smaller grass species (*M. decumbens*) and the comparatively slower-growing woody plant (*A. karroo*) species were unable to match the intense competition from the larger, faster-growing grass species, appear to discredit this model, but rather support the alternative, 'resource pre-emption' model. This latter model states that larger plants usurp resources at the expense of smaller plants because of their ability to secure more than their proportional share of resources as based on their relative size (Weiner and Thompson 1986). Miller and Werner (1987) gave this hypothetical example of the scenario: An asymmetric hierarchy of species or individuals may develop whereby tallest plants may use the resource (e.g. light) unimpeded by other plants, the second tallest may use the light that filters through it, unimpeded by those beneath, and so on. The latter model is supported more strongly by the results of this study because not only were the growth rates of the smaller grass species suppressed by competitors, but these often died when competition intensified as the numbers of neighbours gradually increased (from no neighbours to eight neighbours). As stated by Hutchinson and Budd (1981), when the ability of a plant to compensate for competitive stress via plastic responses is exceeded, mortality occurs.

6.4.2 Competition, disturbance and resource availability

Few ecologists today doubt that competition is an important structuring factor in plant communities, but researchers disagree on the circumstances where it is most intense, and on which traits can be considered to contribute to competitive ability for different species. The distinction between a species' effect on resources and its response to reduced resource levels might help to solve these questions. Clipping reduced the growth of all species to varying degrees, while fertilization enhanced it (Table 6. 3). This demonstrates the fact that irrespective of size plants respond to resource availability as well as disturbance regimes. However, the interaction between these

two factors gives more insight than their main effects. When plants were grown in resource poor soil (0 %), they were greatly suppressed, and clipping significantly reduced their biomass production except for the medium-sized *Themeda triandra*, which exhibited the highest performance (Table 6.4). This indicates that the species, which is arguably the most economically important veld grass species in South Africa (O'Connor 1996), is able to recover from defoliation even at low levels of resource availability. This indeed supports the notion that as a Decreaser species, *T. triandra* thrives under constant but moderate defoliation (Snyman 2004).

In general, larger or broad-leaved species (e.g. *Digitaria eriantha*, *Eragrostis curvula*, *Panicum. maximum* and *Sporobolus fimbriatus*) were suppressed by clipping to a higher magnitude under low soil fertility than the shorter *T. triandra*, *C. plurinodis*, *M. decumbens* and the slower-growing shrub *Acacia karroo* (Table 6.4). For instance, clipping reduced the growth of *E. curvula* by about 78 %, while it reduced *Melica decumbens* by only 42% in the 0 % fertility treatment. Similar results were reported in eastern Ontario by Keddy (et al. 2002), who found out that smaller, narrow-leaved herbaceous species performed relatively better in stress treatment pots than broad-leaved plants, while the broad-leaved species performed better in less intense stress or in the absence of stress.

Increases in soil fertility (50 % and 100 %) conveyed some shifts in the species' competitive response hierarchy: All the species performed better with no clipping, and the taller grasses gained momentum and produced higher biomasses than the smaller grasses. This illustrated directional change in the species' performances across gradients of resource availability and disturbance. The results appear to support the resource-ratio hypothesis of plant succession, which attempts to explain the role of competition for resources by common species in spatially heterogeneous habitats and along spatial gradients (Tilman 1982). The theory also suggests that succession results from a gradient in the relative availabilities of limiting resources over time, thereby implying that changes in resource supply can lead to compositional change or dominance of a particular plant community (Tillman 1985).

Trends in this study showed that the species' competitive ability were inversely related if the species differed in size (i.e. either in height or size of leaves). The taller grasses (*D. eriantha*, *E. curvula* and *P. maximum*) had a competitive edge over the

shorter, narrow-leaved grasses (especially *C. plurinodis* and *M. decumbens*) and the invasive *Acacia karroo*, particularly in high fertility. When the plants were clipped, the shorter species such as *T. triandra* become more competitive than when unclipped or when grown on fertile soil. These shifts in competitive abilities are an indication of trait trade-offs among the species. Similar results were also observed in a study by Fynn (et al. 2005), who observed that the broad-leaved *P. maximum* was the most competitive in fertile soil, while the tall, narrow-leaved *Hyparrhenia hirta* was most competitive in poor soil. These results could be attributed to the fact that when nutrients are more abundant, the taller grasses grow faster and build enough biomass and subsequently usurp the nutrients at the expense of the smaller species. When nutrients become depleted, due to their body size, the smaller grasses are able to persist and perform comparatively better than the taller grass species. Clipping (which is a simulation of grazing intensity), also improved the performances of taller grasses because it reduces shading and improves light interception, so that the species are kept in a more productive, actively-growing state.

Goldberg and Werner (1983) suggested that competitive effect ability is a consistent trait of a species, linked to specific plant traits. Given the fairly consistent hierarchy of competitive effects and responses, what traits determine the species position in a competitive hierarchy? Competitive effects should be related to the plant's ability to deplete resources so they become unavailable to others (Goldberg 1990), hence greater depletion rates should result in greater competitive effects. In this study, the larger-sized plants had higher competitive effects than smaller plants, it therefore appears that plant size was related to the resource-depletion ability. Some differences were however found between competitive species in competitive effect (e.g. *C. plurinodis* vs *T. triandra*), implying that plant size is not the only determinant of competitive effect or the ability to deplete resources. This hierarchy of competitive effects was to some extent determined by relative growth rate, consistent with the hypothesis that all else being equal, the effects of relative growth rate on competitive effect are confounded with growth form (Goldberg and Landa 1991). Hierarchies in competitive responses were slightly more variable than in competitive effects, especially when the phytometers were clipped and fertility level varied. Therefore competitive response does not appear to be related to any noticeable plant trait.

6.4.3 Competitive interactions between species

Interaction among species is central to community ecology (e.g. Schoener 1983, Bruno et al. 2003), and testing hypotheses in community ecology often requires quantification of the magnitude of interactions between species so that these magnitudes can be compared among groups of taxa or of environments (Goldberg et al. 1999). In this study, all the species had negative relative interaction indices (RII's) while growing with both two and eight neighbours, whether the fertility was high or low, and even whether the plants were clipped or not. These negative RII values are indicative of competitive interaction as opposed to facilitation, in which case the RII values would be positive. As highlighted by Armas (et al. 2004), the biomass of individuals growing alone will reach a maximum size determined by their genotype and the environment, but will be smaller if competing with others and larger if the presence of others is facilitative.

Although the species' competition intensity did not vary significantly with clipping, the fact that it increased with fertility and neighbours (Table 6.4) appears to support theories ascribing changes in vegetation along fertility gradients to variation in competition intensity. Results demonstrating this theory were also reported in separate experiments (e.g. Keddy 1989; Keddy et al. 2002; Fynn et al. 2005). However, other studies found no variation in competition intensity with soil fertility (Wilson and Tilman 1993; Campbell and Grime 1991). These contentious results indicate the complexity of interactions because some of the responses may be due to other environmental factors that were not investigated in the experiment.

In this study, *Cymbopogon plurinodis*, *Eragrostis curvula* and *Melica decumbens* exhibited weaker competitive interaction, while *Sporobolus fimbriatus* and *Themeda triandra* showed the highest interaction, signifying that they were being strongly suppressed by neighbours. (Figure 6.2). The differences between the species' competitive interactions may explain species traits and the successional hierarchy or community organization in this semi-arid savanna on which they are commonly found. The two late-successional Increaser I species (*Cymbopogon* and *Melica*), which had low interaction indices, are more shade tolerant and dominate in moribund or overgrown conditions where disturbance is minimal but competition is comparatively

high. The results of this study support the fact that these species become more abundant in the late successional seres where competition is not too intense and disturbance is minimal. *Themeda triandra* is a mid-successional Decreaser species which dominates in moderately grazed, less shaded areas. For this species to persist at this stage of community development, it must be able to perform under intense competition with faster-growing pioneers species and moderate to high disturbance irrespective of soil fertility level. In this study, *Themeda triandra* exhibited stronger competition against the taller or broader-leafed species only when the plants were clipped and growing in poor soil fertility, while the taller, broader-leafed *Digitaria eriantha* and *Panicum maximum* were most competitive when clipped in high fertile soil. These responses appear to support the hypothesis that plants may fully compensate or overcompensate for the removal of tissue by defoliation (Oosterheld and McNaughton 1988): That is, in poor or infertile soil, *T. triandra* channelled more resources towards the replacement of removed foliage, while *A. karroo* and *C. plurinodis* also followed the same pattern in fertile soil.

Panicum maximum and *Digitaria eriantha* showed a modest competitive interaction, and this substantiates the fact that that they are mid-succession species. *P. maximum* which grows well under tree shade and in fertile soils (van Oudtshoorn 1999), was enhanced by fertilization (Table 6.4), but exhibited an overall moderate competitive interaction. The encroaching shrub *Acacia karroo*, whose seedlings compete with grasses in this semi-arid savanna, also exhibited reasonable competitive interaction with grasses. It also exhibited compensatory growth after clipping, implying stimulation by defoliation. These results are consistent with the findings of Stuart-Hill and Tainton (1989), who reported a strong inverse relationship between *A. karroo* height and grass production, as well as a reduction in grass production after clipping *A. karroo* due to its strong competitive effect it exhibits after defoliation. Management implications for this type of rangeland are that moderate defoliation in fertile soil will favour taller grasses, while *T. triandra* will out-perform them in less fertile soils.

6.5 Conclusions

In summary, the experimental results showed that the eight phytometer species differed in their competitive effects and also in their responses to competition, and that their responses varied with clipping and soil fertility. As pointed out by Zedaker (1982), competition is a result of plant density and size relative to available resources. Taller grass species (*Digitaria eriantha*, *Eragrostis curvula* and *Panicum maximum*) generally out-performed the comparatively smaller grasses and the shrub *Acacia karroo*. The study therefore supports the 'resource pre-emption' model, which states that larger plants usurp resources at the expense of smaller plants because of their ability to secure more than their proportional share of resources as based on their relative size. There was evidence of compensatory growth among the species when plants were clipped in poor and highly fertile soil. The taller grass species performed much better when fertility was higher compared to low fertility, and were able to grow fast after clipping. However, when fertility was poor, the taller grasses were more adversely affected than the shorter grasses. Competition was more intense when fertility was higher than at low fertility.

This study has indicated the importance of considering individual plants in modelling or predicting plant competitive responses because as stated by Berger (et al. 2008), plants compete locally, not globally. Based on the results, it can be concluded that disturbance regimes and soil fertility interact to have significant influences on competitive effects and responses of grasses in this vegetation type. It can therefore be concluded that soil fertility, fire and herbivory are important factors that influence the plantsuccession in savannah grasslands.

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CHAPTER 7 GENERAL DISCUSSION AND CONCLUSIONS

7.1 General Discussion

Global demographics indicate that the world population has reached seven billion people, of which one billion are in Africa, and 50 million in the Republic of South Africa (Rosenburg 2011). The need to step up efforts to produce enough food by improving agricultural outputs within the limits of good conservation is apparent. Intensive rangeland improvement such as fertilization, replacement and reinforcements rapidly increase production by 100 to 1000 %, but these are costly and difficult to implement (Trollope 1999). The understanding of how abiotic factors (including climate change) and biotic factors (including human activities) affect individual plants, communities and ecological systems is key in developing 'predictive theory' (Tilman 1998) for optimum production and sustainable management and conservation of plant resources for current and future generations.

Although there is extensive information on fire behaviour and its effects on vegetation, its role in maintaining rangelands in grasslands and savannas has not been fully understood hence over time, its use as a management tool has decreased (Mapiye et al. 2008). This reduction in its use is due to its negative attributes such as temporary elimination of potentially usable forage and destructive effects of breakaway fires in rangelands (Trollope 1989; Bond and van Wilgen, 1996). Both fire and herbivory are strong selective forces in the evolution of the flora of most grasslands and savannas. Therefore, the understanding of the influences of different fire regimes on composition, productivity and soil properties of grazed ecosystems could assist range users to formulate economically viable and ecologically sound strategies of using prescribed burning as a rangeland improvement or rehabilitation tool. Since burning is commonly used to achieve short/medium-term management goals, then:

- What are the long-term ecological and economic consequences of this fire application?
- What precautions should be taken to avoid rangeland deterioration caused by repeated fire application to achieve these important management goals?
- What are the implications of fire application on intensively grazed systems such as communal rangelands?

Scientific reports indicate that succession and competitive interaction play integral roles in maintaining a desirable rangeland condition (Tow and Lazenby 2001). The results obtained from the long-term trial at the University of Fort Hare research farm indicated the role fire plays in succession and species interactions relative to species composition, light interception, aboveground productivity and soil nutrients in this semi-arid savanna. The competition and shade-tolerance experiments also provided some insights on how shading and/or competition for light and soil resources influence succession patterns in this vegetation.

7.1.1 The role of fire in shaping species composition of a South African savanna

The results of the long-term fire trial in Chapter 2 indicated how burning frequency influences succession patterns of herbaceous species over time. Succession in this context is defined as the temporal pattern of vegetation change that can show the change in community types with time, the series of system states or describe the increase and decrease of particular species populations (Pickett et al. 1987). Ordination plots indicated the directions and magnitudes of change in herbaceous species composition in response to 28 years of varying burning frequencies, with some species increasing in abundance while others decrease with increase in burning frequency. The theory of fire-tolerance and intolerance in the life histories of herbaceous species was demonstrated by the changes in the species abundances in response to fire frequency. *Themeda triandra*, a species of very high grazing value and a key indicator of good range condition, was favoured by frequent burning, while *Melica decumbens*, which is of very poor grazing value and becomes abundant in poor range conditions, was gradually eliminated by fire. Most of the other species which might be of moderate grazing value were present at intermediate or low burning frequency. The results also conform that 'Fire is a large, generalist herbivore' that sometimes competes with, sometimes replaces and sometimes facilitates herbivory (Bond 1977; van Wilgen et al. 2003).

Debates on the role of fire in semi-arid savannas not only focus on conservation of fire-sensitive species, but rather on the role of fire on promoting the dominance of some species over others (van Wilgen et al. 2003). The fact that infrequent burning resulted in a more diverse species composition is in conformity with the findings at

Ukulunga research station of the University of KwaZulu-Natal (Fynn et al. 2004). These reports support the theory that intermediate disturbance is necessary for maintaining species diversity (Uys et al 2004). Some Terrestrial Ecosystem Models also state that ‘the size of a disturbance regime that is linked to succession process affects diversity’ (Connell and Slatyer 1977). These models therefore highlight that small scale disturbances are important in creating niche differences and hence support species diversity, as was the outcome of the aforementioned long-term trials. These results that imply that fire can be used successfully to manipulation species composition to a specified range condition, either for livestock production or for conservation. Fire can be used to promote productivity by favouring desirable species and reducing the abundance of undesirable plants (Tainton and Mentis 1984). For instance, in this study frequent burning increased the abundance of desirable species such as *Themeda triandra*, and suppressed undesirable species like *Melica decumbens*. These results bring some insight on the judicial application of fire as a management tool in semi-arid savannas. However, they are of limited application intensive where grazing is practiced. This is because grazing also causes defoliation, but unlike fire, herbivores graze selectively and its effects are not the same as those of fire because the less desirable species are usually not defoliated (Trollope 1983),

In the False Thornveld of the Eastern Cape, a typical African semi-arid savanna where burning is commonly practiced primarily to control undesirable species such as encroaching Karroo, macchia and bush, infrequent burning appears to be a recommended practice. However, the challenges pertinent to burning grazed areas in semi-arid and arid environments are that biomass production is usually low and burning would not always be recommended because it would eliminate the already limited potentially usable forage, as well as reduce vegetation cover and subjecting the area to accelerated soil erosion. Therefore infrequent burning would only be the best practice in conservation areas such as parks and game reserves to keep them pristine.

Although fire interacts with other environmental factors at play in nature (especially grazing in rangelands), the results of this single-factor long-term experiment were able to attest the evolutionary role of fire in maintaining savannas with respect to

burning frequency. The results invariably affirmed the concept of fire-tolerance and intolerance among herbaceous species.

7.1.2 Effects of burning frequency on plant productivity and soil properties

Fire is extensively used as a management tool to simultaneously achieve management goals in southern African grasslands and savannas. The current view on the permissible reasons for burning rangelands is to remove unacceptable/moribund material and control/prevent encroachment of undesirable species. Removal of moribund material is believed to improve access to new growth for herbivores, which would improve animal performance (Bailey 1986). The results in Chapter three (3) show similar trends to those of Chapter two (2) with respect to the effects of burning frequency on light interception and biomass production: Frequent burning and the absence of fire led to a reduction in Leaf Area Index, light interception and the subsequently low biomass production in the long term. The fact that infrequent burning resulted in higher habitat productivity due to improved light interception shows that disturbance regimes such as fire are important in maintaining a more diverse and productive ecological system. Briske and Heitschmidt (1991) reported that primary production decreases mainly because of reduction in the availability of leaf area to intercept solar energy. This is a scenario that is common in frequently disturbed systems such as heavily grazed and frequently burnt areas. Precaution should be taken when applying fire in grazed systems because defoliation by grazers also results in temporary reduction in leaf area to intercept solar energy for photosynthesis.

Fire affects soil moisture, temperature, fertility, infiltration and water-holding capacity (Bond and van Wilgen 1996). Through burning, nutrients which accumulated in the plant biomass get released during combustion, and can become available to plants which grow immediately after a fire, or may be lost due to leaching or volatilization. However, long-term effects of fire are more crucial to the maintenance and sustainability of communities than temporal ones where fire is a natural environmental factor, or where it is repeatedly applied for management purposes. The significant decrease in total C, total N, P and N mineralization with long-term fire

application (Chapter 4) indicated that regular burning caused nutrient loss and a greater nutrient limitation in this semi-arid savanna. These findings are also supported by Clarke (1990) who stated that ‘over longer periods of time the species composition that results from disturbance might impact nutrient supply by influencing total carbon and N pools, element ratios, and pH.

Some studies in a range of ecosystems have shown that plants may use amino acids and other organic N forms in situ. These studies show that some mycorrhizal plants are able to access amino acids, amino sugars, peptides, proteins and even chitin (Bajwa and Read 1985; Finlay et al. 1992; Schimel and Chapin 1996; Kielland 1997; Lipson and Monson 1998; Schiller et al. 1998; Jones and Kielland 2002). It is therefore apparent that organic-N use by plants may be a common phenomenon, at least in systems where nitrogen supplies are limited. There is a possibility that this could be happening in this area because soil N values reported in Chapter 5 are very low. Despite these studies showing that plants in N-poor ecosystems access organic N, it is still unclear how much of a plant's N actually comes directly from organic sources, and also few studies have attempted to quantify the balance of organic vs. inorganic N forms taken up by plants (Schimel and Bennett 2004). This scenario creates an opportunity for further investigation.

Although soil depth did not have significant effect on soil nutrients, soil pH and K generally increased with increase in soil depth, but there was a reduction in Ca, P and N concentrations. The variation in nutrient levels was more pronounced on the top layers (0-2 cm depth). These findings necessitate careful consideration of nutrient dynamics in the soil-plant system where regular burning is administered with the intent to improve the protein content of post-fire vegetation in grazed ecosystems.

Crawley (1997) stated that plant species composition and productivity within a region largely reflect the prevailing climatic conditions. Therefore the interpretation and application of these results are considered in acknowledgement of the presence of other environmental factors that could have significant interaction with disturbance regimes. These include seasonal and annual rainfall as well as temperature, which play an important role in dictating population dynamics over time (Wright and Coleman 1999).

7.1.3 Competitive interactions of key species in a South African semi-arid savanna: The influence of shade, soil nutrients and grazing

As stated in Chapter 1, plant species evolved towards a pattern of resource allocation which minimizes their chances of extinction, and (Oksanen et al. 2006), and such patterns have been retained and refined through the process of natural selection. The resource-allocation pattern of a species determines, in part, its functional address (niche) in a community (Hartvigsen 2000). Therefore, species whose adaptation to the prevailing climatic conditions and soils is superior would make them the competitive dominants of the community under certain conditions of light and moisture (Archer et al. 2004). The results presented in Chapter 5 showed that shading reduces the dry matter production of all grass species, but to varying magnitudes. The taller species were comparatively more sensitive to shade than the shorter ones. They produced higher biomasses in full sunlight than the smaller grasses, but experienced a proportionally higher reduction in dry matter production while generally growing under 50 % or more shade.

From these results, it is apparent that for these species to coexist, each category of species has found its niche in this community's succession hierarchy over evolutionary time. The taller or broadleaved grass species such as *Digitaria eriantha* would normally have a competitive advantage for light over the smaller/shorter species under conditions of uniform or no disturbance (e.g. non-selective grazing or burning, or their absence). It is therefore not surprising that the shorter species such as *Melica decumbens* are less sensitive to shade than taller species and vice versa. The results may also explain rangeland degradation in the form of compositional change which often occurs in mismanaged rangelands through overstocking and understocking of livestock, compared to rangelands utilized by wild herbivores. In nature, uniform utilization of plant species is almost always achieved through the concept of ecological separation, whilst in livestock systems, poor grazing management alters natural light conditions, reduces the relative proportion of desirable species and avails more resources to those less acceptable to livestock. This alters the conditions and niche balances of these species, hence their performances.

Therefore there is need for improved range management to ensure high productivity and persistence of pastorally important grasses in a constantly changing light

environment. The frequency of burn is determined by fuel availability, climatic conditions and an ignition event (Bigalke and Willan), and the best time to burn to produce the desired effects varies with management objectives, and depends on the physiological stages of the plants (Trollope 1989). In highly productive rangelands such as moist grasslands and savannas, the recommended burning frequency is every 3-4 years (van Wilgen et al. 1997), provided the grass fuel load is in excess of 4000 kg/ha. Selective grazing should also be controlled or minimized in these areas so that the large proportion of grasses is grazed, with supplementary feeding where necessary.

Chapter 6 reports differences in competitive effects and responses of selected species under simulated environments of disturbance and soil fertility. As was the case with the shade tolerance experiment, taller species were able to outgrow the shorter ones, hence exerting a competitive advantage, especially in fertile soils with no clipping. Relative Competitive Interaction also increased with soil fertility in the absence of clipping. These results are in conformity with the hypothesis that ‘competition intensity increases with increasing primary productivity and neutral plant-plant relationships prevail in barren areas’ (Oksanen et al. 2006). Disturbance is recognized as an important factor affecting competitive interactions in grasslands and savannas. As stated in Chapter 1, influences of disturbances are superimposed on the background of this topo-edaphic heterogeneity and climatic variability to further influence community-level processes (Archer et al. 2004). In light of this, some shifts in the species’ competitive response hierarchy were observed when the plants were observed: The medium-tall species (*Themeda triandra*) was able to perform better than the comparatively taller species such as *Digitaria eriantha*, *Eragrostis curvula* and *Panicum maximum*, especially at lower soil fertility levels. These observations further demonstrate the co-existence of different plant communities in the same environment, each having found its niche so that it can maximize its fitness to avoid complete exclusion or extinction.

Acacia karroo, a medium-tall shrub or tree species, was included in the competition experiments together with the seven phytometer grass species. The rationale behind its inclusion was due to the significant role the species plays in the structure and dynamics of this semi-arid savanna classified as the False Thornveld of the Eastern Cape (Acocks 1988). This species has encroached large areas of this region and its

seedlings are reported to compete with grass species for moisture and soil resources (Mopipi et al. 2009). Its performance at both juvenile and mature stages is reported to be significantly influenced by environmental factors such as grass competition, drought, fire and herbivores, which affect opportunities for recruitment and establishment of trees (van Langevelde 2003). In these competition experiments, *A. karroo* generally performed poorly and was sometimes outcompeted by grasses to result in mortalities, the results which were similar to those reported by Mopipi (et al. 2009). The implications for range management to promote grass dominance, there should be good grass cover, and the grass should be kept at an actively growing and competitive stage to suppress seedling recruitment of *A. karroo*. Good grazing management should be practiced to avoid overgrazing, which reduces grass vigour and cover.

The results of the competition experiments also imply to a large extent, that species are able to coexist even under intense competition for resources in very short supply. Could there possibly be a positive feedback mechanism among these species, perhaps some positive interaction such as facilitation? Plants can actively change the environmental conditions of themselves and their neighbours (e.g. Stoll and Weiner, 2000). Some modifications can make it easier for other plant individuals to establish, grow, survive, and reproduce. Such modifications are termed facilitation (Berger et al. 2007). Facilitative mechanisms may however act simultaneously with negative interactions such as resource competition or even allelopathy, and the overall effect of one species on another may be the product of multiple complex interactions. Positive interactions may also determine community's spatial patterns, permit coexistence, enhance diversity and productivity, and drive community dynamics (Callaway II 1995). Considering the low levels of soil nutrients in this system from the long-term trial, some form of positive feedback mechanism such as facilitation may be at play which could explain the species coexistence in this area. This creates yet another opportunity for future research.

7.2 General Conclusions

Grazed and burnt ecosystems are generally complex, decision-making processes should be based on knowledge of animal and vegetation ecology, hydrology and animal nutrition/husbandry. Each landscape property is unique in terms of resources, land form, economic stability and managerial skill. (Danckwerts et al. 1993). Over the past 50 years, rangeland scientists in the USA, South Africa and Zimbabwe conducted grazing studies and devised a variety of grazing systems designed to convert plant communities from a low ecological state to a higher and more productive and palatable state (e.g. Heitschmidt and Taylor 1991; Danckwerts et al. 1993; Heady and Childs 1994). The goal was not to improve harvest/grazing efficiency, but to change vegetation composition through rotational grazing and resting, a practice that was extensively adopted in South Africa and North America (Pieper and Heitschmidt 1988).

Recent reviews on some of the dogma associated with such grazing systems have shifted emphasis towards the overriding impact of stocking, spatial distribution of grazing, animal type, fire and tactical resting (Stuth et al. 2000). Much attention is now given to using 'short-duration' high stocking densities in conjunction with rotational grazing systems especially in higher rainfall areas (Stutha and Marschin 2000). However, not all resource managers are interested in livestock production alone. Some environmental organizations are also interested in using fire and livestock grazing to manage biodiversity. They have realized that in some areas, through heterogeneous distribution of livestock, grazing can alter competitive relationships to enhance diversity through differential disturbance of preferred species (Milchunas et al. 1988; Fuhlendorf and Smeins 1996). This approach, to my view, is a good example of sustainable conservation agriculture.

The primary objective of the studies were to investigate the roles of competition and disturbance on plant community dynamics in terms of species composition, light interception, primary productivity and soil nutrients in a South African semi-arid savanna called the False Thornveld of the Eastern Cape. The objective was achieved because based on the results obtained from the long-term trials at the University of

Fort Hare, and the experiments conducted, a number of conclusions were drawn, and recommendations made for sustainable range management as outlined below:

From results obtained using the long-term fire trial at the University of Fort Hare research farm, burning can have both negative effects and positive effects on this vegetation from a range and conservation standpoint. These attributes are summed up in the conclusion by Phillips (1965): 'fire is a bad master but a good servant.' This is evidenced by the fact that on the positive side, frequent burning enhanced the dominance of fire-tolerant *Themeda triandra*, which has good grazing value. However, this in the long-term occurred at the expense of intolerant species such as *Melica decumbens*, which was dominant in the absence of fire but was gradually reduced by frequent burning. The abundances of forb and karroid species were also reduced by frequent burning. The elimination of fire-intolerant species are positive from a range management standpoint, but for biological conservation and long-term ecological sustainability of the area. Frequent burning (annual and biennial burns) and the absence of fire also resulted in a less variable plant community after 28 years, with a few dominant species, while less frequent burns (3-6 years) produced a more variable species composition consisting of both fire-tolerant and fire-intolerant herbaceous community. The absence of fire promoted the abundance of species that are of good forage value, and since grazing was excluded from the trial, this signifies that infrequent burning could be used as a management practice to improve composition and enhance biodiversity in this area.

Frequent burning and an absence of fire in the long-term lead to reduction in Leaf Area Index, light interception and a reduction in aboveground biomass production. Conversely, infrequent burning increased Leaf Area Index, improved light interception into grass canopies and increased aboveground biomass production in the long term. Moreover, frequent burning resulted in an increase in soil pH, K, Ca, and Na, while it decreased total C, total N, the C: N ratio P and N mineralization. The implication for rangeland management therefore, is that ignoring effects of other factors such as grazing and rainfall, burning after 3-6 years appear to be the most suitable fire frequencies to apply when using fire as a management tool in the False Thornveld of the Eastern Cape. In the absence of grazing pressure, infrequent burning would not only enhance species composition, but would improve light interception,

herbage production and also enhance soil conservation by positive feedback on soil properties. Considerable attention should also be given to studies on soil nutrient dynamics in grazed and burnt areas.

There was considerable variation in the degrees of shade tolerance between common species of this semi-arid savanna: *Digitaria eriantha* and *Eragrostis curvula* were most adversely affected by shading, hence are classified as highly shade intolerant, while *Melica decumbens* was not significantly affected by shade, and is hence classified as shade tolerant. *Cymbopogon plurinodis*, *Panicum maximum*, *Sporobolus fimbriatus* and *Themeda triandra* are classified as moderately shade-tolerant. The study also showed that some species can perform better in partial shade than in full sunlight, but shading of 70 % or more would adversely affect performances of most grasses from this semi-arid savanna. An implication for sustainable range management is that appropriate gap size for satisfactory natural regeneration and seedling growth of savanna or open grassland species would therefore require a gap large enough to provide at least 30 % of ambient light. This would entail burning in moist grasslands and savannas and good grazing management practices to avoid overgrazing.

Competitive effects and responses of grasses in this vegetation type were highly influenced by soil fertility, fire and grazing. There were some shifts in competitive effect and response hierarchies in responses to the simulated environmental variables. Taller grass species (e.g. *Digitaria eriantha*, *Eragrostis curvula*, *Panicum maximum*) generally suppressed or out-competed the shorter grasses (especially *Melica decumbens*) in nutrient-rich soils, but their performances were more adversely affected when fertility was poor compared to the shorter grasses. Relative Competition Intensity was generally higher when fertility was high than at low fertility. The results indicate that the effects of grazing on species performances are often confounded with soil fertility, and this is in conformity with the statement by Zedaker (1982), that ‘competition is a result of plant density and size relative to available resources.’

Theory suggests that successful species must have either a low response to the abundance of other species, and/or a large enough effect that the abundance of other

species is significantly reduced. Therefore, a species may either have a low response and a high effect, or any other combination of effect and response. One of the range management objectives in this area is to promote the abundance of *Themeda triandra*, which is of high forage value and an indicator of rangeland that is in good condition. The general situation under livestock farming conditions in the False Thornveld is that if the grass sward is optimally grazed and rested then there is a great potential for *Themeda triandra* to dominate (Mathews 1956). The results of the competition experiments indicated that the species exhibits strong competitive interaction, and also exhibited stronger competitive effect after clipping in low fertility. Although its biomass production was generally lower than that of *Digitaria eriantha*, *Eragrostis curvula* and *Panicum maximum* (which can be attributed also to genotype), this high relative interaction and competitive effect means that if the grazing areas are managed properly, *T. triandra* can remain highly vigorous/competitive. These results imply that it has a low response and a high effect, a trait that would enhance its performance if it is moderately grazed or the area is burnt. The species is also moderately shade tolerant, and this may explain why it thrives in burnt and moderately grazed areas.

These studies have demonstrated the complexity of community structure and function, and how the environment and mismanagement can lead to degradation in the form of compositional change and reduction in habitat productivity. The studies have inevitably demonstrated the importance of considering individual plants in modelling or predicting plant competitive responses because plants compete locally, not globally. As proposed, the recommendations would contribute towards enhancing knowledge on these issues.

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APPENDICES

Appendix 1 Analysis of variance (ANOVA) output for the shade tolerance trial

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
BLOCK stratum	5	52.686	10.537	1.40	
BLOCK.*Units* stratum					
Species	6	1086.537	181.090	24.14	<.001
Shade	4	754.146	188.536	25.13	<.001
Species.Shade	24	320.926	13.372	1.78	0.019
Residual	170	1275.330	7.502		
Total	209	3489.625			

Appendix 2 Table showing results for ANOVA and Tukey's test for the (Log) mass of phytometer species in the competitive response plot trial

Source of variation	d.f. (m.v.)	s.s.	m.s.	v.r.	F pr.
BLOCK stratum					
FERT	1	6.20859	6.20859		
BLOCK.FERT stratum					
FERT	1	0.27638	0.27638	2169.83	0.014
Residual	1	0.00013	0.00013	0.00	
BLOCK.FERT.*Units* stratum					
SPECIES	7	60.11260	8.58751	149.96	<.001
COMP	2	13.15149	6.57575	114.83	<.001
CLIPPING	1	1.28620	1.28620	22.46	<.001
FERT.SPECIES	7	0.39649	0.05664	0.99	0.439
FERT.COMP	2	0.01702	0.00851	0.15	0.862
SPECIES.COMP	14	1.16935	0.08352	1.46	0.127
FERT.CLIPPING	1	0.02371	0.02371	0.41	0.521
SPECIES.CLIPPING	7	0.05762	0.00823	0.14	0.995
COMP.CLIPPING	2	0.00158	0.00079	0.01	0.986
FERT.SPECIES.COMP	14	0.65817	0.04701	0.82	0.646
FERT.SPECIES.CLIPPING	7	0.14751	0.02107	0.37	0.920
FERT.COMP.CLIPPING	2	0.02509	0.01254	0.22	0.803
SPECIES.COMP.CLIPPING	14	0.27863	0.01990	0.35	0.987
FERT.SPECIES.COMP.CLIPPING	14	0.24915	0.01780	0.31	0.992
Residual	268 (18)	15.34760	0.05727		
Total	365 (18)	88.23309			

Tukey's 95 % confidence intervals (Variance = 0.0573 with 268 degrees of freedom)

Mean	- Mean	Lower	Difference	Upper	significant
E	A	-0.3231	-0.1739	-0.0247	Yes
E	B	-0.7533	-0.6041	-0.4549	Yes
E	H	-0.8963	-0.7471	-0.5978	Yes
E	G	-0.9481	-0.7988	-0.6496	Yes
E	C	-1.0181	-0.8688	-0.7196	Yes
E	D	-1.2702	-1.1209	-0.9717	Yes
E	F	-1.3586	-1.2093	-1.0601	Yes
A	B	-0.5795	-0.4302	-0.2810	Yes
A	H	-0.7224	-0.5732	-0.4239	Yes
A	G	-0.7742	-0.6249	-0.4757	Yes
A	C	-0.8442	-0.6949	-0.5457	Yes
A	D	-1.0963	-0.9470	-0.7978	Yes
A	F	-1.1847	-1.0355	-0.8862	Yes
B	H	-0.2922	-0.1429	0.0063	No
B	G	-0.3440	-0.1947	-0.0455	Yes
B	C	-0.4139	-0.2647	-0.1155	Yes
B	D	-0.6661	-0.5168	-0.3676	Yes
B	F	-0.7545	-0.6052	-0.4560	Yes
H	G	-0.2010	-0.0518	0.0974	No
H	C	-0.2710	-0.1218	0.0275	No
H	D	-0.5231	-0.3739	-0.2246	Yes
H	F	-0.6115	-0.4623	-0.3131	Yes
G	C	-0.2192	-0.0700	0.0793	No
G	D	-0.4713	-0.3221	-0.1729	Yes
G	F	-0.5597	-0.4105	-0.2613	Yes
C	D	-0.4013	-0.2521	-0.1029	Yes
C	F	-0.4898	-0.3405	-0.1913	Yes
D	F	-0.2376	-0.0884	0.0608	No

Appendix 3 Results for ANOVA and Tukey's test table for Relative Interaction

Indices of species

Source of variation	d.f.	(m.v.)	s.s.	m.s.	v.r.	F pr.
BLOCK stratum	1		0.22749	0.22749	9.46	
BLOCK.FERT stratum						
FERT	1		0.02638	0.02638	1.10	0.485
Residual	1		0.02406	0.02406	0.44	
BLOCK.FERT.*Units* stratum						
SPECIES	7		1.75879	0.25126	4.63	<.001
COMP	1		3.36814	3.36814	62.06	<.001
CLIPPING	1		0.09711	0.09711	1.79	0.183
FERT.SPECIES	7		0.81337	0.11620	2.14	0.042
FERT.COMP	1		0.03802	0.03802	0.70	0.404
SPECIES.COMP	7		0.33027	0.04718	0.87	0.532
FERT.CLIPPING	1		0.02526	0.02526	0.47	0.496
SPECIES.CLIPPING	7		0.13225	0.01889	0.35	0.930
COMP.CLIPPING	1		0.00105	0.00105	0.02	0.889
FERT.SPECIES.COMP	7		0.36672	0.05239	0.97	0.458
FERT.SPECIES.CLIPPING	7		0.22446	0.03207	0.59	0.763
FERT.COMP.CLIPPING	1		0.00151	0.00151	0.03	0.868
SPECIES.COMP.CLIPPING	7		0.14761	0.02109	0.39	0.908
FERT.SPECIES.COMP.CLIPPING	6	(1)	0.18893	0.03149	0.58	0.746
Residual	171	(19)	9.28090	0.05427		
Total	235	(20)	16.57354			

Tukey's 95 % confidence intervals (Variance = 0.0543 with 171 degrees of freedom)

Mean	- Mean	Lower	Difference	Upper	significant	
G	H	-0.1992	-0.0205	0.1583	No	
G	C	-0.2947	-0.1159	0.0628	No	
G	F	-0.3034	-0.1246	0.0541	No	
G	A	-0.3305	-0.1518	0.0270	No	
G	E	-0.3351	-0.1564	0.0223	No	
G	D	-0.3578	-0.1790	-0.0003	Yes	
G	B	-0.4580	-0.2793	-0.1005	Yes	
H	C	-0.2742	-0.0954	0.0833	No	
H	F	-0.2829	-0.1041	0.0746	No	
H	A	-0.3100	-0.1313	0.0475	No	
H	E	-0.3146	-0.1359	0.0428	No	
H	D	-0.3373	-0.1586	0.0202	No	
H	B	-0.4375	-0.2588	-0.0801	Yes	
C	F	-0.1874	-0.0087	0.1700	No	
C	A	-0.2146	-0.0358	0.1429	No	
C	E	-0.2192	-0.0405	0.1383	No	
C	D	-0.2419	-0.0631	0.1156	No	
C	B	-0.3421	-0.1634	0.0154	No	
F	A	-0.2059	-0.0271	0.1516	No	
F	E	-0.2105	-0.0318	0.1470	No	
F	D	-0.2332	-0.0544	0.1243	No	

F	B	-0.3334	-0.1547	0.0241	No
A	E	-0.1834	-0.0046	0.1741	No
A	D	-0.2060	-0.0273	0.1515	No
A	B	-0.3063	-0.1275	0.0512	No
E	D	-0.2014	-0.0226	0.1561	No
E	B	-0.3016	-0.1229	0.0558	No
D	B	-0.2790	-0.1002	0.0785	No

Identifier	Mean			
G	-0.4675			
H	-0.4470			
C	-0.3515			
F	-0.3428			
A	-0.3157			
E	-0.3111			
D	-0.2884			
B	-0.1882			

Appendix 4 ANOVA table of (log) mass of phytometers for the pot trial

Source of variation	d.f.	(m.v.)	s.s.	m.s.	v.r.	F pr.
BLOCK stratum	4		1.1312	0.2828	0.63	
BLOCK.FERTILITY stratum						
FERTILITY	2		4.4545	2.2273	4.93	0.040
Residual	8		3.6147	0.4518	2.33	
BLOCK.FERTILITY.SPECIES stratum						
SPECIES	7		34.6145	4.9449	25.48	<.001
FERTILITY.SPECIES	14		5.6710	0.4051	2.09	0.022
Residual	74	(10)	14.3617	0.1941	1.90	
BLOCK.FERTILITY.SPECIES.*Units* stratum						
CLIPPING	1		4.4201	4.4201	43.38	<.001
FERTILITY.CLIPPING	2		0.9797	0.4898	4.81	0.011
SPECIES.CLIPPING	7		2.6719	0.3817	3.75	0.002
FERTILITY.SPECIES.CLIPPING						
Residual	12	(2)	3.0261	0.2522	2.47	0.010
Residual	65	(31)	6.6234	0.1019		
Total	196	(43)	57.8624			

Appendix 5 ANOVA table for (log) mass of neighbours for the pot trial

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
BLOCK stratum	4	3793.1	948.3	4.20	
BLOCK.FERTILITY stratum					
FERTILITY	2	209699.6	104849.8	464.06	<.001
Residual	8	1807.5	225.9	1.67	
BLOCK.FERTILITY.SPECIES stratum					
SPECIES	7	9929.6	1418.5	10.51	<.001
FERTILITY.SPECIES	14	13334.0	952.4	7.06	<.001
Residual	84	11338.5	135.0	0.51	
BLOCK.FERTILITY.SPECIES.*Units* stratum					
CLIPPING	1	70888.3	70888.3	265.45	<.001
FERTILITY.CLIPPING	2	9354.4	4677.2	17.51	<.001
SPECIES.CLIPPING	7	18013.7	2573.4	9.64	<.001
FERTILITY.SPECIES.CLIPPING	14	14172.2	1012.3	3.79	<.001
Residual	96	25636.4	267.0		
Total	239	387967.5			