EFFECTS OF RAIN, NITROGEN, FIRE AND GRAZING ON BUSH ENCROACHMENT IN SEMI-ARID SAVANNA, SOUTH AFRICA

Tineke Kraaij

Thesis presented in partial fulfilment of
the requirements for the degree of Master of Science
at the University of Stellenbosch

Supervisor:
Prof. David Ward

December 2002

Declaration

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

Signature: Date: ...20 August 2002...

ABSTRACT

Increases in woody plant density ('bush encroachment') reduce livestock production and biodiversity. By convention, soil moisture, soil nutrients, fire and herbivory are regarded as the principal factors governing the tree-grass ratio of savannas. An experiment with a completely-crossed design was employed to investigate woody seedling (*Acacia mellifera*) recruitment near Kimberley, Northern Cape, South Africa, after fire and under conditions of maximum-recorded rainfall, nitrogen addition and grazing. The field experiment was repeated as a garden experiment to determine if the two experiments yield comparable results.

Tree germination in the field was extremely low, probably due to below-average natural rainfall in plots that only received natural rain, and insufficient watering frequency in irrigated plots. As a result of low germination, none of the treatments (rain/nitrogen/fire/grazing) had a significant effect on tree recruitment in the field experiment. The duration of the experiment (2000/2001 growing season) was insufficient for the treatments to affect grass composition, although the high rainfall treatment and grazing exclusion significantly improved grass cover and height. The garden experiment showed that frequent watering, no nitrogen addition and grass clipping significantly enhanced tree germination and survival (termed 'recruitment'). There were also significant interactions among rain, nitrogen and grazing in their effects on tree recruitment. The effects of rain on tree recruitment were more pronounced under nitrogen supplementation and *vice versa*. Similarly, high rain and high nitrogen enhanced the effect of grazing on tree recruitment.

It is inferred that above-average rainfall years with frequent rainfall events are required for mass tree recruitment. Tree seedlings can further benefit from space and resources which are made available through grass defoliation. Conversely, nitrogen enrichment improves the competitive ability of the fast-growing grasses relatively more than that of the N_2-fixing tree component, thereby suppressing tree recruitment. In contrast to conventional wisdom that grazing alone causes encroachment, it is suggested that there are complex interactions between the abovementioned factors and 'triggering' events such as unusually high rainfall.

Contrary to many claims that equilibrium models are inappropriate for explaining savanna dynamics, it was shown that consumer-resource theory has explanatory power for bush-grass dynamics of the savanna studied. The state-space approach that was used facilitated the understanding of savanna dynamics and enabled predictions about the system's response to perturbations. The applicability of consumer-resource theory to semi-arid nutrient-poor savannas confirmed the importance of resource competition in structuring natural systems.

Key Words: Bush encroachment, tree-grass interaction, tree recruitment, *Acacia mellifera*, rain, nitrogen, fire, grazing, consumer-resource theory.

3

OPSOMMING

Toenames in die digtheid van houtagtige plante ('bosverdigting') verlaag veeproduksie en biodiversiteit. Volgens konvensie word grondvog, grondvoedingstowwe, vuur en beweiding beskou as die belangrikste faktore wat die boom-gras verhouding van savannas bepaal. 'n Volledig-gekruisde ("completely crossed") eksperiment is ontwerp om boomsaad-ontkieming (*Acacia mellifera*) naby Kimberley, Noord-Kaap, Suid-Afrika, te bestudeer na 'n brand en onder toestande van maksimum-aangetekende reënval, stikstof toevoeging en beweiding. Die veldeskperiment is herhaal as 'n tuineksperiment om vas te stel hoe resultate van die twee eksperimente vergelyk.

Boomsaad-ontkieming was uiters laag in die veld, waarskynlik weens ondergemiddelde reënval in persele wat slegs natuurlike reënval ontvang het, en 'n te lae benattingsfrekwensie in die besproeide persele. As gevolg van lae ontkieming in die veldeksperiment, het geen behandeling (reënval/stikstof/brand/beweiding) boomsaad-ontkieming beduidend geaffekteer nie. Die duur van die eksperiment (2000/2001-groeiseisoen) was te kort vir die behandelings om grassamestelling te beïnvloed, alhoewel besproeiing en geen beweiding die grasbedekking en -hoogte betekenisvol verhoog het. Die tuineksperiment het getoon dat boomsaad-ontkieming en vroeë oorlewing (genoem 'vestiging') betekenisvol verhoog is deur gereëlde benatting, geen stikstof toevoeging en die sny van gras. Daar was ook beduidende interaksies tussen reën, stikstof en beweiding in hul invloed op boomvestiging. Die reënbehandeling het 'n groter uitwerking op boomvestiging gehad onder stikstoftoevoeging en *vice versa*. Hoë reënval en stikstoftoevoeging het ook die invloed van beweiding op boomvestiging versterk.

Die afleiding is dat bogemiddelde reënvaljare met gereëlde reënbuie 'n vereiste is vir grootskaalse boomvestiging. Boomsaailinge kan verder voordeel trek uit die spasie en hulpbronne wat beskikbaar raak wanneer gras ontblaar word. Daarteenoor verhoog stikstofverryking die mededingendheid van die vinnig-groeiende grasse meer as dié van die N_2-bindende boomkomponent, met die gevolg dat boomvestiging onderdruk word. In kontras met die konvensionele veronderstelling dat beweiding opsigself bosverdigting veroorsaak, word voorgestel dat ingewikkelde interaksies plaasvind tussen die bogenoemde faktore en ander 'sneller-gebeurtenisse', soos buitengewoon hoë reënval.

In teenstelling met baie aansprake dat ekwilibrium modelle ontoepaslik is om savanna-dinamika te verklaar, is getoon dat die verbruikers-hulpbron teorie ("consumer-resource theory") oor verklaringsvermoë beskik vir boom-gras dinamika van die savanna wat bestudeer is. Die staat-spasie ("state-space") benadering gebruik, het begrip van savanna-dinamika bevorder en voorspellings moontlik gemaak aangaande die sisteem se reaksie op versteurings. Die toepaslikheid van verbruikers-hulpbron teorie vir semi-ariede, nutriënt-arm savannas bevestig dat kompetisie vir hulpbronne 'n sentrale rol speel in die strukturering van ekologiese sisteme.

Sleutelwoorde: Bosverdigting, boom-gras interaksie, boomvestiging, *Acacia mellifera*, reën, stikstof, vuur, beweiding, verbruikers-hulpbron teorie.

4

CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

GENERAL INTRODUCTION

a.   Thesis Structure

In this section the layout of the thesis is explained, followed by a general introduction to the phenomenon of bush encroachment, including the rationale and objectives of this study. The study area is then briefly described (additional information on the study area is presented in the Materials and Methods of Chapters 2 & 3) after which a more detailed description of the study species is given.

To determine the effects of the most important determinants of savanna structure on the initial stages of bush encroachment, field and garden experiments were conducted. The field experiment was set up at Pniel Estate (situated between Kimberley (28°45' S, 24°45' E) and Barkly West (28°32' S ,24°31' E), Northern Cape, South Africa) to examine the effects of rain, fire, nitrogen and grazing on early tree recruitment as well as their effects on grass composition and biomass. The garden experiment was set up at Stellenbosch University Campus (Stellenbosch (33°55' S, 18°52' E), Western Cape, South Africa) and only investigated early tree recruitment and excluded fire as a treatment.

The structure of this thesis is as follows:
- *Chapter 1* is an extensive literature review on the factors affecting bush encroachment in semi-arid savannas, with emphasis on southern Africa and *Acacia* species;
- *Chapter 2* concerns tree seedling recruitment in both field and garden experiments;
- *Chapter 3* describes grass dynamics in the field experiment; and
- *Chapter 4* explores the application and validity of a mechanistic model of interspecific competition for semi-arid nutrient-poor savannas (including the system studied).

With the exception of the references, which were put at the end of the thesis, the chapters were all written as independent papers (accounting for some replication), authored by T. Kraaij and D. Ward. Despite this independence, each chapter is a contribution to the central issue of the thesis, i.e. the influence of the major factors affecting tree-grass dynamics (encompassing bush encroachment) in semi-arid savanna.

b. Rationale & Objectives

Historical increases in woody plant density with concomitant changes in herbaceous cover and composition (termed 'bush encroachment') have been documented in savannas worldwide (Kreuter *et al.* 1999, Johnson *et al.* 1993). Bush encroachment may be seen as a natural process and in ecological terms merely a progression in plant succession from a lower to a higher stage. However, high tree-grass ratios are of global concern (Skarpe 1990a) because they result in considerable reductions in livestock carrying capacity (Dean & Macdonald 1994; Joubert 1966), thereby negatively affecting commercial enterprises as well as communal and subsistence societies. Bush encroachment also has potentially important ramifications for biodiversity (because the system changes towards a monoculture) (Dean *et al.* 1999), wildlife habitat conservation, nutrient cycling (Scholes & Walker 1993), soil erosion, water infiltration (Walker *et al.* 1981) and desertification (Condon 1986a).

The structure and function of semi-arid savannas are principally governed by soil moisture, soil nutrients, fire and herbivory, the latter two agents acting partly by influencing the availability of and competition for water and nutrients (Teague & Smit 1992; O'Connor 1985). The conventional two-layer model of tree-grass coexistence in savannas (Walter 1971) assumes that trees monopolize water and soil nutrients in the deep soil layer while grasses outcompete trees for these resources in the upper soil layer. Under this scenario, grasses outcompete trees until heavy grazing removes the grasses and facilitates mass tree recruitment. In spite of the above explanation, it still is not understood why tree species may encroach in some areas and not in others despite similar levels of grazing, rainfall and fire (Jeltsch *et al.* 2000 and see Chapter 1).

Simple explanations of the causes of bush encroachment have in many situations been found to be inappropriate, many theories have not been experimentally tested (Van der Schijff 1964), experiments have often been done without replication and results are site- or species-specific (see Chapter 1, 'Overall trends'). In particular, the mechanisms of interaction between the role-playing factors are not well understood (Jeltsch *et al.* 1997), because ecologists have (mostly due to logistical constraints) tended to investigate the role-playing factors independently rather than interactively (O'Connor 1994). In addition, the role of 'triggering' events that might initiate or drive transitions is not adequately known (Archer 1996). Also, greenhouse studies may not be reliable measures of field conditions because different soil properties (compaction, organic matter content, nutrient status etc.) may confound the results.

To address some of the above shortcomings, this study focused on identifying the factors and/or combinations thereof, that create ideal conditions for the initial stages of bush encroachment (i.e. 'triggering' events). We* regarded tree recruitment (early establishment) as the most influencial process in the course of bush encroachment and neglected post-establishment dynamics in our study on account of the following:

(1) inevitably, germination and seedling establishment are prerequisites for an increase in tree abundance;

(2) stands of trees/bush often comprise discrete cohorts, demonstrating the importance of infrequent and large-scale recruitment events (Donaldson 1967a; Booth 1986; Condon 1986a; Harrington & Hodgkinson 1986; Skarpe 1990b; Wiegand *et al.* 2000a). Especially in the case of long-lived species, such as savanna trees, population size frequency distributions often largely reflect recruitment events, while environmental variation has little influence on post-establishment survival (Wiegand *et al.* 2000a);

(3) under ranching conditions in dry areas, fuel loads are generally too low to support fires, and those few fires that occur are not sufficiently frequent and intense to have a significant and lasting destructive effect on mature trees (Du Toit 1972a; Trollope 1982; Bond & Van Wilgen 1996; Higgins *et al.* 2000); and similarly

(4) browsing is unlikely to have significant negative effects on established trees because browsing intensity is too low to affect tree survival (Lay 1965; Stuart-Hill & Tainton 1988, 1989), and browsers are often absent from commercial ranches.

We employed two similar experiments, a field and garden experiment, to determine whether these yield comparable results. If garden experiments prove to be representative of field conditions, they would be the preferred method of experimentation because garden studies are relatively cheap, are easily manipulated and due to the smaller scale, have more scope for investigating many factors and interactions. We also critically reviewed the existing literature on experiments investigating the factors affecting bush encroachment, and evaluated it in light of the mentioned shortcomings.

The specific objectives of this study were:

- to investigate woody seedling (*Acacia mellifera*) recruitment after fire and under conditions of excessive rainfall, nitrogen addition and grazing;
- to contribute to the development of management guidelines for communal and commercial ranchers that will allow them to minimize the occurrence of bush encroachment, thereby optimizing agricultural productivity and biodiversity.

---

* This thesis is written as papers, jointly authored by my supervisor, hence the use of the plural.

10

This study forms part of a broader and longer-term project that aims to provide guidelines for the sustainable management of savannas, using the ranches at Pniel (Northern Cape) as its main study arena. Pniel provides a unique opportunity to study these issues because of the diversity of savanna types and the two management styles (communal and commercial) in place there. Due to vastly different objectives and financial resources of the communal and commercial ranches, it is necessary to produce management guidelines that are feasible for both management types.

c.   Study Area: Pniel Estate

Pniel Estates are situated in the Northern Cape Province of South Africa, close to Barkly West and 35 km north west of Kimberley. The land is 22 000 ha in area and bordered by the Vaal River to the north and the west. Pniel Estates are owned by the Evangelical Lutheran Church of South Africa and the land-use currently comprises commercial game and cattle ranching. This study was carried out in the section of the farm where cattle are run. Prior to 1960, the land was hired out and heavily grazed (often called 'overgrazed' in ranching systems) by various livestock, whereafter a multi-camp system was put into place and since then almost exclusively grazed by cattle on a rotational basis at 8 ha per large stocking unit. Adjacent to Pniel Estates is Pniel communal ranch (3000 ha), occupied by 150 families of black pastoralists who have always lived there and are in the process of gaining it formally from the Evangelical Lutheran Church as a result of a successful land claim. Cattle and goat ranching are the main activities of these communal pastoralists.

The specific selection of three study sites (A, B and C) at Pniel Estates was governed by the proximity of (limited) water sources and patchy distribution of the focus species, *Acacia mellifera*. The underlying rock at site A is andesite, in places amygdaloidal and/or porphyritic, while red aeolian dune sand predominates at sites B and C (Bosch 1993). This sand (95 % quartz) was most likely blown in from the Kalahari to the north of the study area, although some is local in origin (Bosch 1993). The soil type at Pniel varies from moderately deep (0.3 – 0.6 m) to deep (> 0.6 m) red and yellow sands (Hutton, Clovelly and Kimberley soil forms) to shallow (< 0.3 m) and stony (Mispah, Prieska and Glenrosa soil forms) (Bezuidenhout 1994, 1995).

The study area forms part of the summer rainfall area of South Africa and the climate can be described as semi-arid. The mean annual rainfall for Barkly West is 388 mm and rainfall among years is extremely variable (C.V. = 39 %) (Fig. A). Most precipitation occurs in the form of thunderstorms between January and March, with very little rain between May and October (Fig. B). Daily maximum temperatures exceed 30 °C in summer, while for the remainder of the year the days are warm, and the nights in winter are cold (Fig. B) (Van Riet & Louw 1999).
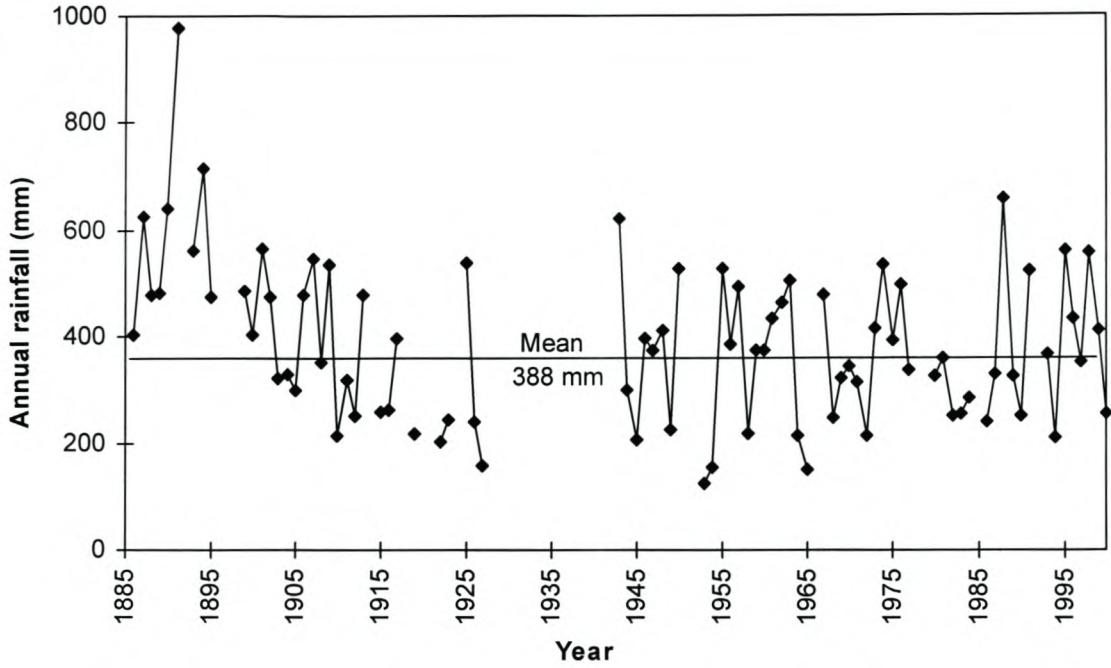
Figure A: Long-term record of annual rainfall for Barkly West (1886 - 2000). Discontinuities in the line indicate unavailable or unreliable data (data obtained from South African Weather Bureau).
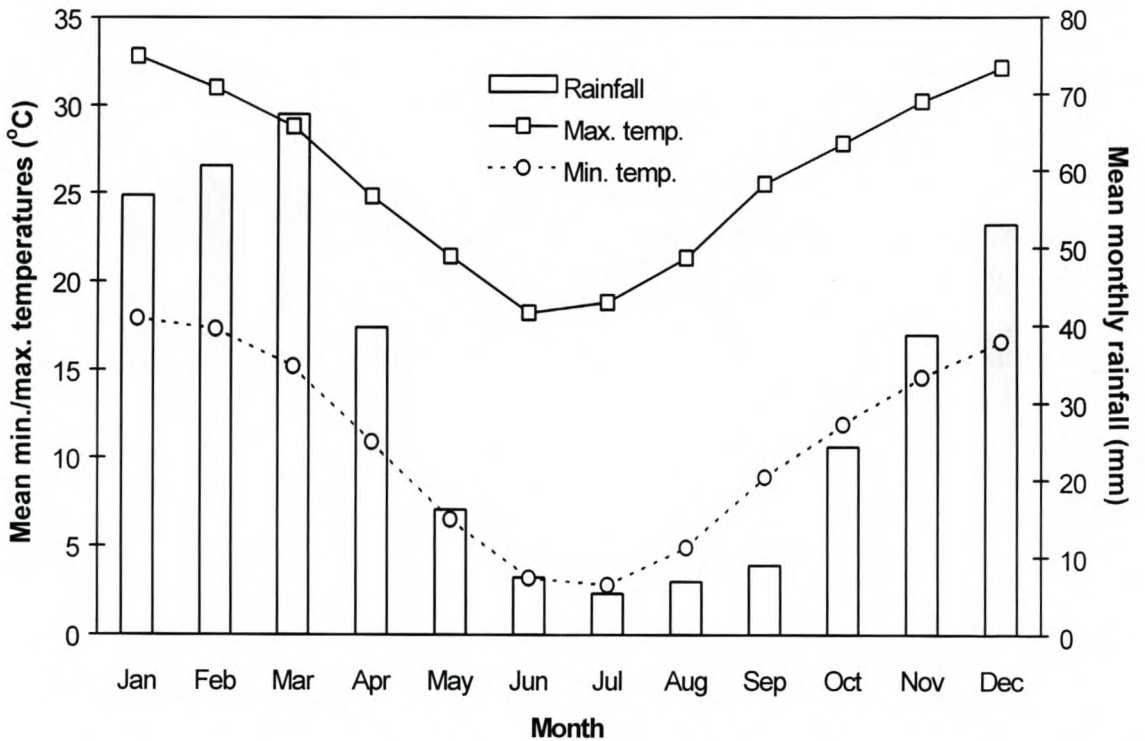
Figure B: Climate diagram showing mean monthly rainfall for Barkly West (1884 - 1999) and mean daily minimum and maximum temperatures for Kimberley (1961 - 1990). Temperature records of Barkly West were not complete for the same time period (data obtained from South African Weather Bureau).

12

d.   Study Species: *Acacia mellifera* (Blackthorn / 'Swarthaak')

Vast areas of important agricultural/pastoral land in southern Africa are subject to severe encroachment by *Acacia mellifera* (Vahl) Benth. subsp. *detinens* (Burch) Brenan (Leguminosae) [syn. *Acacia detinens* (Burch.) Brenan] (Kelk & Donaldson 1970; Palmer & Pitman 1972). In northern Namibia alone, about 10 million hectares are encroached (Holz & Schreuder 1989) and it is also the dominant encroaching tree at the study area in the Northern Cape. *A. m. detinens* is found in Tanzania and southwards to Angola, Namibia, Botswana, the Free State, Northern Cape, Northern Transvaal and North-West provinces of South Africa. This thorny shrub or small tree occurs in dry thornveld, bushveld and wooded grassland (Ross 1979) and is common on inselbergs in the Northern Cape and Namibia, and on the red dunes of the Kalahari. It may grow on a variety of soil types, from sands through heavy clayey soils, or among stones. In sandveld, it is often associated with calcium-rich soils on drainage lines (Smit 1999). *A. mellifera* can withstand frost (Palmer & Pitman 1972) and its distribution matches annual rainfall zones between 200 mm and 500 mm, with the average mean annual rainfall in its range in the Northern Cape and Namibia being *c.* 300 mm per annum (Donaldson 1967a).

A. mellifera is capable of symbiotic N_2-fixation (Moshe *et al.* 2000) and seedlings also bear root nodules (Adams 1967). In a study comparing eleven different species of the Mimosaceae family (including nine southern African *Acacia* species, *Prosopis glandulosa* and *Dichrostachys cinerea*), Schulze *et al.* (1991) found that *A. mellifera* had the highest contribution (71 %) of N_2-fixation to the total nitrogen content of leaves. The plant possesses a shallow but extensive lateral root system, extending 8 – 15 m from the stem, parallel to the surface and at a depth of 25 cm (Adams 1967; Skarpe 1990a), supported by a deep tap root which makes it less dependent on surface moisture (Donaldson 1967a). Leaf fall begins in January and the tree remains bare until September or October. *A. mellifera* should be most sensitive to defoliation (and thus browsing and mechanical control) in October after the first growth flush, for which stored carbohydrates are mobilized (Milton 1987). Chemical control on the other hand, is most effective in March (Van Niekerk & Kotze 1977) as poisoning depends on translocation of photosynthate to the roots, which is correlated with leaf-fall. *A. mellifera* briefly bursts into a mass of cream-coloured flowers when borne on shoots produced the previous year in spring (Milton 1987). The flowers are very attractive to bees – hence, the specific epithet *mellifera*, meaning 'honey-bearing' (Smit 1999). The paired hooked thorns are small and inconspicuous, but some of the most effective of all the many *Acacia* thorns – hence, the subspecific epithet *detinens*, the Latin 'detinere' meaning 'to detain/hold'. The pods are flat and papery and mature quickly, are shed in summer or autumn and are wind dispersed (Carr 1976). The fresh seeds of wind-dispersed species usually germinate readily after rain (Tybirk *et al.* 1993).

In tree form, *A. mellifera* is valuable for fodder, fuel wood and shade (Palmer & Pitman 1972). Together with the young twigs, leaves and flowers, the pods are nutritious and eaten by domestic stock (sheep and goats in particular) as well as by kudu. Although the pods and leaves are sometimes consumed, the carrying capacity of the veld is reduced by an increase in tree density (Joubert 1966). Like most *Acacia* species, blackthorn produces coppice shoots from the stems whenever the top growth is damaged (Donaldson 1967a), but repeated damage to shoots can reduce regrowth in the following season (Milton 1987).

A. mellifera grows gregariously and can cover the field (spreading by coppice and seed), forming impenetrable, tangled, thorny thickets (Adams 1967; Palmer & Pitman 1972). Consequently, the ground flora is often sparse (Donaldson 1967a) – too sparse to carry fires into the thickets and thus they are considered fireproof (Adams 1967). Isolated bushes are also difficult to burn because the branches and leaves of young or mature bushes form dense, hemispherical masses, touching the ground all around the stems. A fire will scorch the leaves and the ends of the twigs, but will not reach the main stem (Jackson 1955 op.cit. Adams 1967). Old moribund trees have a more tree-like form because the lower branches die, allowing grasses to grow underneath and making it more susceptible to fire. Although fire, as control measure for *A. mellifera*, was often found to be ineffective due to the species' resprouting ability, Donaldson (1967b) showed that a total root kill (which prevents subsequent coppicing) could be obtained by burning the lower basal stem(s) of the plant for at least three minutes.

A. mellifera often gives the impression that the bushes are of the same age (uniformly low stature) over large areas (Donaldson 1967a; Skarpe 1990b). The establishment of such cohorts might correspond to rare years of ideal moisture conditions (*cf.* Booth 1986; Condon 1986a; Harrington & Hodgkinson 1986; Wiegand *et al.* 2000a). Another explanation for stands of uniform stature may be found in the spatial and temporal pattern of competition between crowded shrubs (Wiegand *et al.* 2000b; Skarpe 1990b). The trees' ages are not easily determined because *Acacias* exhibit sub-annual growth rings (Adams 1967). Consequently, Adams (1967) estimated the relative ages of trees based on their combined height and shape, and instead of uniform tree ages within stands, he found a normal age frequency distribution inside the thickets and an irregular distribution outside thickets.

It has been noted in Namibia (Joubert 1966) and South Africa (Kraaij *pers. obs.*) that *A. mellifera* encroachment may be very patchy. Patchy encroachment may be accounted for by differences in soil types, e.g. Joubert (1966) found encroachment on mountain loam soils, but not on deeper

14

sandy soils. The high spatial variation in rainfall (low mean annual precipitation is related to high spatial and temporal variance, Sharon 1981) may also correspond with the distribution of woody thickets, where localized rainfall events provided ideal conditions for establishment at any particular point in time.

Holz and Schreuder (1989) reported on a dieback disease in Namibian populations of *A. mellifera* that reached epidemic proportions at the time of writing, ascribed to different fungi (four *Phoma* species and *Cytospora chrysosperma*) and possibly stress-initiated. Since blackthorn is considered as a drought-tolerant plant (Joubert 1966), the initiating stress factor(s) remained obscure. The feasibility of using fungi as biological control agents should be investigated.

1. LITERATURE REVIEW: THE FACTORS INFLUENCING BUSH ENCROACHMENT WITH EMPHASIS ON SEMI-ARID AND ARID SAVANNAS IN SOUTHERN AFRICA

1.1 Abstract

Savanna vegetation structure is principally governed by rainfall, nutrients, fire, herbivory and their interactions. Whether savannas are transient or stable equilibrial systems is controversial. The two-layer model explains tree-grasses coexistence by niche separation: grasses obtaining water and nutrients from the topsoil and trees from the subsoil. Tree establishment may be limited by rainfall frequency, while grasses are more limited by nitrogen than leguminous trees. Fire destroys juvenile trees but also frees space and resources available for tree recruitment. Heavy grazing similarly creates favourable conditions for tree establishment by depressing grass growth and resource consumption. Conversely, heavy browsing damages trees and tree seedlings, thereby benefiting the grasses. The phenomenon of bush encroachment (increased tree-grass ratio) globally reduces savanna profitability and biodiversity. In addition to the effects of the governing factors on tree-grass competition, increased tree seed dispersal by livestock and global climate change may contribute to bush encroachment. Control measures for bush encroachment are often unsuccessful in the long term and expensive.

Keywords: Population dynamics, tree-grass ratio, grazing, rainfall, fire, nutrients, browsing, overall trends, equilibrium.

1.2 Introduction

Savanna vegetation covers just under one third of the earth's land surface (Skarpe 1991), over half the area of Africa and Australia, 45 % of South America, about 10 % of India and South-East Asia, and 2 % of North-America (Werner *et al.* 1990; Scholes & Archer 1997). Semi-arid savanna regions (< 400 mm p.a.) constitute more than a third of the South African savannas (Low & Rebelo 1998). Overall, savannas contain a large and rapidly growing proportion of the world's human population, as well as the majority of its rangelands and livestock (Skarpe 1991; Scholes & Archer 1997). Most savannas are experiencing increasing pressures from demographic and economic changes that have increased dramatically over the past few decades (Werner *et al.* 1990). In addition, the forecasts of global climate change, that may result in altered species composition (Midgley *et al.* 1998), further alert us to conserve and manage wisely the savanna ecosystems of the world.

Savannas vary considerably in their structure, ranging from a few scattered trees in grasslands to closed woodlands consisting mostly of trees and little grass. Thus, savannas are delineated structurally (specifically, they have a woody-grass composition) but also climatically (a distinct wet and dry season) (Bate *et al.* 1982; Werner *et al.* 1990). The structure and function of savannas is principally governed by soil moisture, soil nutrients, fire and herbivory, the latter two agents acting partly by influencing the availability of and competition for water and nutrients (O'Connor 1985; Teague & Smit 1992). However, the many levels of interaction among the various determinants of savanna structure complicate the matter considerably. Conventional wisdom posits that the tree-grass ratio depends on a competitive balance for the various resources (Walter 1971; Walker *et al.* 1981).

Historical increases in woody plant density with concomitant change in herbaceous cover and composition (termed 'bush/shrub encroachment') have been documented in savanna areas worldwide (Johnson *et al.* 1993; Kreuter et al. 1999; Scholes & Walker 1993), including Africa (Kelly & Walker 1976; Van Vegten 1983; O'Connor 1985; O'Connor & Crow 2000), Australia (Walker & Gillison 1982; Booth 1986; Condon 1986a; Harrington & Hodgkinson 1986), North and South America (Buffington & Herbel 1965; Blackburn & Tueller 1970; Hobbs & Mooney 1986; McPherson *et al.* 1993) and India (Singh & Joshi 1979). Bush encroachment is a natural process and, in ecological terms, comprises a progression in plant succession from a lower to a higher serial stage (Trollope 1980). However, a high tree-grass ratio considerably reduces the profitability of savanna systems (Du Toit 1972b) because both cattle and sheep are primarily grazers. Consequently, woody plant encroachment is of considerable socioeconomic concern, as it contributes to reductions in livestock carrying capacity (Joubert 1966; Du Toit 1968; Milton & Dean 1995; Jeltsch *et al.* 1997) due to lower grass production and reduced access for cattle if the encroaching species are thorn trees (Wiegand *et al.* 2000c). Bush thickening thus negatively affects commercial enterprises, pastoral societies and subsistence cultures in arid and semi-arid environments (Heady 1975; Burrows *et al.* 1985) where other forms of agriculture are not possible on account of the low and erratic rainfall. Bush encroachment into grasslands and savannas also has potentially important ramifications for biodiversity (because the system tends to a monospecific community) (Vitousek *et al.* 1996; Dean *et al.* 1999), wildlife habitat conservation, nutrient cycling (Scholes & Walker 1993), water infiltration (Walker *et al.* 1981), soil erosion (Schlesinger *et al.* 1990) and desertification (Condon 1986a).

A variety of factors may have prevented bush encroachment before the modern era of high density livestock farming (Downing 1978; Madany & West 1983) e.g. fire, browsing, mechanical damage by large wild ungulates (Walker et al. 1981), dispersal limitations for tree seeds (Archer *et al.* 1988;

Archer 1989), grass competition, insects, plant diseases, meteorological phenomena (unseasonal frost / climate changes / seasonal shifts in precipitation) (Nielson 1986; Archer 1989; Weltzin *et al.* 1997), low human population densities due to disease and human activities (e.g. slash-and-burn agriculture) (Trollope 1980). It has also been proposed that global atmospheric CO_2 enrichments may be driving bush encroachment (Johnson *et al.* 1993).

An understanding of the extent and cause of changes that have occurred in savanna systems encroached by trees/shrubs are necessary (*cf.* Jeltsch *et al.* 2000) if we are to mitigate future undesirable impacts of bush encroachment, and realistically assess restoration potentials. One of the objectives of rangeland management is to stabilize the vegetation at the most economically meaningful stage in plant succession. Generally, under ranching conditions this stage is either grassland or open savanna, because profitability is measured in terms of the quantity of grass available for livestock/game species.

We will now introduce the four major determinants of savanna structure i.e. herbivory (divided into grazing and browsing), fire, rainfall and nutrients (Schultz *et al.* 1955; Frost *et al.* 1985; Knoop & Walker 1985; Van Auken *et al.* 1985; Walker & Knoop 1987; Stuart-Hill & Tainton 1988, 1989; Teague & Smit 1992; Jeltsch *et al.* 1996; Van Wilgen & Scholes 1997; Higgins *et al.* 2000) as well as some aspects of global climate change (Johnson *et al.* 1993). Table 1.1 summarizes the results of various studies on the effects of the determinants of savanna structure on the tree-grass ratio. Thereafter the influences of trees on their environment and the process of tree recruitment will be examined. A discussion of different models of equilibrium/stability will integrate the concepts dealt with. We will also touch on control measures before drawing a few conclusions.

1.3   Grazing

Radical changes to semi-arid savanna vegetation in Africa since European settlement have been ascribed to the introduction of domestic livestock (Downing 1978; Walker *et al.* 1981). The most pronounced effects of grazing have been recorded in the semi-arid regions of southern Africa (O'Connor 1985). Many studies have shown that an increase in woody plant density follows sustained heavy grazing (Van Vegten 1983; McPherson & Wright 1990; Skarpe 1990a,b; Smit & Rethman 1992; Schultka & Cornelius 1997). Stuart-Hill and Tainton (1988, 1989) attributed it to the fact that frequent grazing stimulates browse production, possibly by reducing resource utilization by grasses (Harrington & Hodgkinson 1986). Contrastingly, Andersson (1856), Du Toit (1972a) and Brown and Archer (1989) provide evidence counter to the still widely-held opinion that long-term and/or heavy grazing is a prerequisite for bush encroachment (Joubert 1966; Madany &

18

West 1983; Scholes & Walker 1993). In general, studies about the effects of grazing on bush encroachment and grass performance produced mixed results, e.g. Strang (1974) found that light grazing accelerated the process of bush encroachment, while heavy grazing promoted a dense grass sward. Du Toit (1972b) showed evidence of retrogression in the composition and cover of the grass sward in the Eastern Cape due to rotational (heavy) grazing by sheep as opposed to continuous (lighter) grazing by sheep, while Smit and Rethman (1992) found the opposite to be true for cattle grazing in the Sourish Mixed Bushveld. From the above it is clear that grazing is not necessarily the overwhelming factor causing bush encroachment.

To summarize, grazing appears to have two contrasting effects on savanna herbaceous vegetation: a decrease in perennial palatable species, total production and cover often as a result of intense grazing, as opposed to an increase in palatability, and maintenance of production and cover due to moderate grazing. Possible explanations for increased herbaceous production as a result of grazing are lower water requirements of a grazed sward, and consequently lower water stress, and higher nutrient availability as nutrient turnover rates are increased by herbivores (Skarpe 1991; also see 'Nutrients'). The negative effects of grazing on rangelands, however, has a snowball effect: the increase in size and density of unpalatable plants (woody/herbaceous) due to grazing, further intensifies grazing pressure on the remaining palatable herbaceous plants (e.g. Smit & Rethman 1992). Therefore, as woody plants become established, new successional processes and positive (self-reinforcing) feedbacks can drive the system to a new state (Archer *et al.* 1988; Milton *et al.* 1994; Archer 1996).

The two disparate effects of grazing on grass performance (i.e. enhanced *vs* reduced grass biomass production) are essentially what the overcompensation debate (compensatory growth hypothesis) is about (McNaughton 1979a,b; Belsky 1986; Belsky *et al.* 1993a). Several investigators claimed that herbivory can benefit plant species' productivity, longevity or reproductive potential (see reviews by McNaughton 1979b and Belsky 1986). In other words, some plants respond positively to injury, by replacing lost tissue to varying extents. However, Belsky (1986) showed that strong evidence for improved grass performance as a result of grazing is lacking (apart from under growth-chamber conditions and in cultivated crops). In the long term, plants have to bear the cost of loss due to herbivory. In instances where grazing stimulated above-ground grass production in the short term (e.g. Stuart-Hill & Tainton 1988), below-ground reserves have probably been depleted to achieve this. Accordingly, Van Auken and Bush (1989) showed that clipping reduced belowground grass biomass more than above-ground biomass.

The effects of grazing (and other factors) on tree-grass dynamics is usually explained in terms of an alteration in the competitive ability of grasses *vs* trees in acquiring resources (Walker *et al.* 1981; Fowler 1982; Frost *et al.* 1985; Stuart-Hill & Tainton 1988; Cohn *et al.* 1989; Davis *et al.* 1998). Stuart-Hill and Tainton (1988) emphasized the complexity of the tree-grass system, with interactions between grazing and browsing pressure on the one hand, and grass and browse production on the other, complicated by bush density (see 'Tree influence on understory'). These authors showed that moderate browsing stimulated browse production, resulting in increased competitive ability of trees, which in turn suppressed grass production. Grazing also reduced the competitive ability of grass, thereby further promoting tree performance. It appears as though both moderate grazing and browsing lead to a reduction in grass vigour and stimulation of browse production. However, overuse of either component leads to an increase in the production of the other (Stuart-Hill & Tainton 1988, 1989) because vigour, and thus consumption of the overused component is reduced, thereby making resources availble for use by the remaining vegetation. Grazing and fire cessation are also inextricably intertwined: grazing causes a reduction in fine fuel, and hence a reduced likelihood of burning, which exacerbates the problem of enhanced woody seedling survival (in the case of no post-germination fires) (Madany & West 1983).

Jeltsch *et al.* (1997) obtained disconcerting results from a simulation experiment in the Kalahari, in that stocking rates currently recommended by pasture scientists in southern Africa have a high probability of bringing about shrub encroachment within a century. Apart from controlling livestock numbers at an ecologically sustainable level, the objective for pastoralists should be to sustain more diverse (various grazers and browsers) and dynamic herds. This should increase flexibility in the utilization of different vegetation components in response to environmental and vegetational changes (Skarpe 1991) and contribute towards securing production and biodiversity.

1.4   Fire

Fire can influence the success of woody seed viability and germination (Bradstock & Auld 1995; Babalwa & Witkowski 1997), either by breaking seed dormancy of hard seeded species or by causing mortality of less robust seed (Bond & Van Wilgen 1996). It is necessary to differentiate between the influence of fire on the existing community and the potential recruitment following fire. Post-germination fires favour the development and maintenance of a predominantly grassland vegetation by destroying juvenile trees and shrubs or by stunting the growth of multi-stemmed adult shrubs (so-called 'Gullivers', Bond & Van Wilgen 1996), thereby preventing the development of more mature plants to a taller fire resistant stage (Du Toit 1972a; Trollope 1974, 1980; Lacey *et al.* 1982; Roberts 1986). With infrequent burning due to low fuels or no ignition sources, 'Gullivers'

periodically escape, resulting in an increase in the bush-grass ratio (Bond & Van Wilgen 1996). Once the bush has become dominant and suppresses the grass, fire is no longer effective because insufficient grass fuel is present to support an intense fire (Trollope 1980). Accordingly, the characteristic aggregation of savanna trees in clumps can in some instances be ascribed to the decreased fire probability and intensity within clumps which reduces damage to seedlings (Menaut *et al.* 1990; Jeltsch *et al.* 1996). Based on the same principle, fire can only be effective as a control measure during the initial stages of bush encroachment or as a follow-up treatment after the eradication of the original stand of encroaching bush (Adams 1967; Trollope 1974). Pre-germination fire, on the other hand, may facilitate tree recruitment by reducing above-ground grass biomass and therefore competition with tree seedlings (Schultz *et al.* 1955; Bond & Van Wilgen 1996). Depending on the tree species and fire intensity, burning may also either facilitate germination by breaking seed dormancy, or prevent germination by destroying tree seeds with softer seed coats (Bradstock & Auld 1995; Babalwa & Witkowski 1997).

In addition to its effect on trees, fire may be responsible for changes in the composition of the herbaceous layer (Medina & Silva 1990). A change in grass composition may, in turn, limit bush encroachment, provided that the fire regime favours perennial grasses at the expense of annual pioneer species (Joubert 1966). Joubert found the denser, more permanent cover of perennial grasses to be more resistant to tree recruitment than an annual sward. Burning in different seasons has different effects on bush-grass dynamics. In summer-rainfall areas, fire during the growing season (i.e. late spring and summer) has deleterious effects on actively growing grasses, and as a consequence, early-spring burns are usually recommended to improve perennial grass vigour (Joubert 1966; Trollope 1980, 1987). However, fires after the first spring rains are not hot enough to control bush encroachment (Trollope 1987). Thus, in summer-rainfall areas, very intense fires to control bush are best obtained at the end of winter before the first spring rains when grasses are still dormant (Trollope 1987).

In South Africa, the use of fire as a means to control bush encroachment has often been unsuccessful due to the failure to recognize the various roles fire plays in moist and arid savannas (Trollope 1980). In the arid savannas, rainfall is too low and erratic to support fires that are frequent and intense enough to prevent the regeneration of bush from coppice and seedling growth (Trollope 1982; Higgins *et al.* 2000). Even in the event of fierce burns, plants as young as a year old may survive destruction of top growth (Du Toit 1972a). As a consequence, the ecological role of fire in controlling bush encroachment in arid savannas should merely be to retard woody growth and to maintain bush at an available height and in an acceptable state for browsing animals (Trollope 1974; Scholes & Walker 1993). Although fires in arid or semi-arid savannas are less

common than in mesic savannas, they are also important because they usually occur after a good rainy season, which coincides with tree seedling establishment events (Van Rooyen *et al.* 1991). In addition to the interaction between rainfall and fire, grazing also interacts with fire, and many of the effects of fire are likely to vary depending on the presence or absence of grazers (Hobbs *et al.* 1991). Grazing reduces fire intensity and frequency by removing grass biomass (i.e. fuel) and selective grazing increases spatial heterogeneity in the behaviour of fire (Hobbs *et al.* 1991).

1.5   Rainfall

The importance of rainfall for tree-grass dynamics led to Walter's (1971) two-layer soil-water hypothesis: grasses are superior competitors for water in the topsoil, while woody plants have exclusive access to lower (subsoil) water supply. If this holds true, then factors that promote water percolation to deeper soil layers, e.g. stony soils, winter rains (Stuart-Hill *et al.* 1986) and longer-duration rainfall events should favour the tree component, and therefore, bush encroachment. Contrary to the two-layer hypothesis, it was shown that tree roots and grass roots exploit essentially the same soil volume and that grasses are able to utilize subsoil water (Knoop & Walker 1985; Noy-Meir & Walker 1986). However, Knoop and Walker (1985) found the highest densities of grass roots to be in the topsoil, suggesting that the grass layer obtains most of its water from this zone. In addition, the rate of subsoil water use by trees exceeded that of grasses. Therefore, the two-layer model can still operate in instances of root-overlap, provided each vegetation component is the superior competitor in a different layer. Yet, this may sometimes not be the case. Wiegand *et al.* (2000c) found that bush encroachment occurred on soils too shallow to allow for root separation. BenDavid-Novak and Schick (1997) showed that woody species are often at least as dependent on surface flows as on groundwater. In particular, woody species with shallow lateral roots can make optimal use of topsoil water and small showers (Skarpe 1990b). The phenomenon of hydraulic lift (i.e. tree roots exuding water, drawn from deep moist soil-layers, in the drier surface soil, Caldwell & Richards 1989) further reduces the possibility of separate tree and grass rooting-niches. The two-layer model is also not valid if we consider the early establishment phase of trees in a grass matrix: if grasses were the superior competitors for surface-soil water, they would always be able to suppress tree recruitment and even prevent germination (during the stage when tree seedlings share the same soil volume), which is not the case. It is clear that there are many instances in which the two-layer model is too simplistic.

Bush encroachment, as a particular state of tree-grass coexistence, may be explained on the basis of temporal (phenological) rather than spatial (depth) niche separation of trees and grasses (Scholes & Walker 1993). Leaf production by grasses is usually scattered throughout the growing

season, while woody plants often achieve full leaf expansion early in the season, in addition to retaining leaves for several weeks after grasses have senesced (Scholes & Archer 1997). The early- and late-seasonal growth of trees likely depend on carbohydrate reserves rather than on current photosynthate (Rutherford & Panagos 1982). As a result, trees could monopolize water from the early and late rains, while grasses are more competitive in the mid-rainy season (Rutherford & Panagos 1982; Scholes & Walker 1993, also *cf.* Skarpe 1990b). Roux (1966) described the opposite phenomenon in the Karoo, i.e. early 'grass rains' and later 'shrub rains'. In general, Scholes and Archer (1997) predicted dominance by trees wherever seasonality is strong, protracted and predictable, whereas grasses with their opportunistic growth strategy would be favoured in arid unpredictable environments dominated by small rainfall events (Soriano & Sala 1983). However, for both the temporal and spatial niche separation models, many local exceptions occur. The concepts of phenology and depth are also not unrelated because having a deep root system, which allows access to the reliable water supply of aquifers, is linked to the ability of rapid/early leaf expansion and extended leaf retention into stress periods (Scholes & Archer 1997).

Knoop and Walker (1985) predicted that competition for soil water among trees and grasses would be greatest in years of average rainfall, and that woody plants would be favoured in very wet years. Therefore, the effect that the herbaceous layer has in limiting bush encroachment would be moderated by variation in annual rainfall. In a simulation experiment, Jeltsch *et al.* (1997) showed that higher rainfall stochasticity at sites with a lower mean annual precipitation is reflected in higher stochasticity of shrub encroachment at these sites. Climatic variability and the unpredictable occurrence of extreme climatic events may effect rapid shifts in plant recruitment and mortality. These may unexpectedly promote grass dieback and/or trigger tree seed production, dispersal or seedling establishment (Archer 1996). Large-scale shrub recruitment events due to above-average rainfall have been recorded by various authors (e.g. Booth 1986; Condon 1986a; Harrington & Hodgkinson 1986). The latter also ascribed extension, thickening-up and re-establishment of thickets (after fire) to consecutive years of heavy rainfall. The positive effect of above-average rainfall on woody growth may be enhanced by destruction of perennial grasses during preceding drought accompanied by severe grazing (Du Toit 1972a).

Wilson and Witkowski (1998) determined that frequent, but not necessarily high, rainfall was essential for germination and early seedling survival of four African *Acacia* species. Frequent (even small) rainfall events may promote seedling establishment more effectively than fewer large rainfall events. In fact, large rainfall events without follow-up rains can result in the destruction of the majority of seeds (99.5 % in *A. mellifera*, Donaldson 1967a) which disintegrate upon drying after inibition. It is likely that ideal conditions (i.e. frequent smaller rainfall events) are only episodically

23

met, probably during above-average rainfall periods, during which cohorts of seedlings may establish, with long periods of time where no or very few seedlings establish.

Southern African farmers often assert that a decline in the mean annual rainfall and/or changing rainfall patterns in the semi-arid areas (Andersson 1856; Vogel 1988b) are responsible for land degradation, including woody plant invasion. However, there is no evidence of progressive change in rainfall amount/patterns in South Africa during the past 150 years (Vogel 1988a,b). There has rather been a change in the effectiveness of the rainfall, caused by changes in infiltration rates of soil as a result of trampling (Dean 1992) and increased runoff due to the removal of vegetation and the loss of topsoil (Snyman & Fouché 1991).

Medina and Silva (1990) point out that rainfall and climatological approaches frequently do not take the soil properties in a given area into account. Savanna soils appear to regulate primary production potential because of their low natural fertility, but also their texture and depth frequently affect water availability and duration of the growing period. On finer-textured soils, grasses have a greater effect on subsoil water and woody performance (Noy-Meir & Walker 1986). This is explained by slower water infiltration rates on finer-textured soils, resulting in extended exposure of grass roots to water and increased uptake by grasses. Contrastingly, higher recruitment and therefore higher tree densities can be expected on moderately drained soils with medium to high water tables and long rainy seasons. As mean plant-available moisture duration declines, recruitment should depend on the occurrence of flush germination taking place during wetter years of lower mortality (Medina & Silva 1990).

Various studies, both long- and short-term, have emphasized the overriding influence of rainfall on grass composition (O'Connor 1985) and production (Stuart-Hill et al. 1987) in that it makes the influence of other factors, such as shading, litter, grazing etc. appear relatively insignificant. Any effect of rainfall on grass composition or production may in turn affect the competitive ability of the herbaceous layer vs the tree/shrub component, and ultimately alter the tree-grass ratio.

1.6   Nutrients

The ratio of topsoil to subsoil nutrients may influence tree-grass dynamics in a similar fashion to soil water in the two-layer hypothesis. However, the inherent negative relationship between water availability and nutrient status makes it very difficult to separate these two properties (Knoop & Walker 1985; Smith & Goodman 1986). Water also interacts with nutrients in that nutrients are mineralized, transported and taken up by roots only in the presence of water. Heavy rains early in

the growing season should be optimal for nutrient uptake by grasses (Walker & Knoop 1987), which have a limited storage capacity for nutrients (Scholes & Archer 1997). Contrastingly, early growth of trees (which often precedes the rains) is enabled by their capacity to store and internally recycle nutrients (Scholes & Walker 1993). Therefore, trees should have prior access, not only to water, but also to nutrients mineralized during the early part of the growing season. This trend should be moderated to a limited extent by hydraulic lift (see above), whereby tree roots release water and mineralized nutrients, drawn from the subsoil, in the surface soil, making it available for grasses to use.

Nitrogen availability is limited both by the accumulated pool in the soil and its rate of mineralization, while nitrogen deficiency may be aggravated by the recurrence of fire (Coutinho 1982; Medina 1982a,b; Holt & Coventry 1990; Skarpe 1991; Collins & Steinauer 1998). Frequent burning can stimulate primary production in the short term but also decrease annual plant uptake of nitrogen and result in long-term losses of nitrogen (Blair et al. 1998). Nitrogen losses ascribed to burning may again be significantly ameliorated by the stimulatory effect that phosphate, deposited in the ash following a fire, has on both symbiotic and associative N_2-fixation (Eisele et al. 1989; Blair et al. 1998). Grazing also interacts with nitrogen in that grazers increase rates of nitrogen cycling (Holland & Detling 1990; Holland et al. 1992; Frank & Evans 1997). Grazing-induced soil enrichment stimulates grass growth which leads to further grazing, leading to 'grazing lawns'/'hot spots' (McNaughton 1984, 1986; Skarpe 1991).

Of all nutrients, nitrogen elicits the greatest response from veld in terms of herbaceous composition and production (Grunow et al. 1970; Le Roux & Mentis 1986; Walker & Knoop 1987; Belsky et al. 1993b), but at high levels of nitrogen application a phosphorus deficiency arises. According to Tolsma et al. (1987), phosphorus is the most limiting nutrient in the Botswanan semi-arid savanna due to the strong retranslocation of phosphorus (as opposed to nitrogen) from Acacia leaves to twigs. High rates of abortion of infloresences in Acacia species may also be ascribed to phosphorus deficiency. According to Donaldson and Kelk (1970) the extremely low phosphorus content of the sandy soils of the Northern Cape limits grass growth to a greater extent than anywhere else in South Africa. Although phosphorus is worth more consideration than simply mentioning its importance, this study will concentrate on the influence of nitrogen in savanna dynamics. Our focus is biased towards nitrogen because nitrogen is generally the most limiting nutrient to plant growth (Liebig's law, Russell 1961) and particularly relevant to the dynamics of N_2-fixing trees vs non N_2-fixing grasses. Also, see 'Tree influence on understory' for the effect of trees on levels of soil nutrients other than nitrogen.

It is expected that the symbiotic N_2-fixing ability (through symbiosis with *Rhizobium* bacteria on their roots) of many trees and shrubs in savannas (Schulze *et al.* 1991) greatly contribute to their success in the poor sandy soils, as is the case with alien *Acacia* species in oligotrophic fynbos soils (Roux & Middlemiss 1963; Milton 1980; Dart *et al.* 1991). Tolsma *et al.* (1987) attributed the success of shallow-rooted *Acacia* species in particular, relative to deep-rooted species, in encroaching heavily grazed areas, to better access to nutrients and root symbionts in the surface soil. Smit and Swart (1994) showed that leguminous trees had distinctly higher grass yields under their canopies than under non-leguminous trees or between tree canopies. However, studies comparing soil nitrogen levels beneath the canopy of leguminous and non-leguminous trees, failed to show significant differences between them (Belsky *et al.* 1989, 1993b). Similarly, Garcia-Moya and McKell (1970) found that leguminous plant material was not significantly greater in nitrogen content than that of nonleguminous shrubs. Nitrogen status neither differed significantly between soils of an *Acacia* woodland and soils under grassland (Adams 1967). Although (nonleguminous) grasses are not capable of symbiotic N_2-fixation, some forage grasses, e.g. *Panicum* species and a *Brachiaria* species, have been shown to fix N_2 through association with free-living cyanobacteria (Tjepkema & Burris 1976; Morris *et al.* 1985; Miranda & Boddey 1987; Eisele *et al.* 1989; Chalk 1991). However, quantities of nitrogen fixed through this association may be small when compared to other sources of nitrogen input such as symbiotic N_2-fixation by legumes and atmospheric inputs (Brejda *et al.* 1994). Belsky (1994) suggested that the higher nitrogen status of subcanopy soils compared to intertree areas is due to animal droppings, air-borne deposits and inputs of tree litter not necessarily associated with N_2-fixation by the trees.

In broad-leafed African savanna, the rate of nutrient cycling is 1.2 - 2.4 times faster through the herbaceous layer than through the woody component, suggesting that grasses have a rapid and variable nutrient cycle as opposed to a slower, more stable cycle of trees (Frost 1985). Based on the differences between the herbaceous and woody layer in terms of nutrient cycling rate, nutrient storing capacity and N_2-fixing ability, it can be expected that an increase in soil nitrogen should be more beneficial to grasses than to the tree component. However, there is the danger of changing, and often losing, diversity (Roux & Warren 1963; Mills 1964; Grunow *et al.* 1970; Tainton 1984; Seastedt *et al.* 1991). The phenomenon of reduced diversity due to nutrient enrichment, has been termed the 'paradox of enrichment' (Rosenzweig 1971) or intermediate-productivity hypothesis, stating that diversity is maximized at intermediate productivity (Grime 1979), whereas diversity is limited by competition at both high and low levels of productivity. This pattern has been observed in a wide variety of terrestrial (and aquatic) habitats (Tilman 1982; Van Andel & Van den Bergh 1987), although exceptions occur, e.g. Walker and Knoop (1987) showed that species composition was unaffected after four years of fertilizer application.

1.7 Browsing

The net effect that defoliation will have on a tree will depend on where the plant material is removed, the degree of defoliation and the degree of stress following defoliation (Teague 1983). Numerous studies indicate the importance of herbivory to tree seedling density and recruitment (e.g. Boyd 1988; Borchert et al. 1989). Young trees are physiologically more vulnerable to defoliation, because they do not have reserves to rely on for recovery, and are thus the ideal target for bush control (Teague 1983). Browse generally has a relatively high mineral and protein content, with smaller seasonal variation than grasses (Skarpe 1991). Preferential grazers (e.g. cattle) will often browse when the early growing season for trees coincides with the late dormant season for grasses (Skarpe 1991). Continuous browsing was found to restrict bush competition and improve grass cover, composition and vigour (Du Toit 1972b; Fierro et al. 1986; Teague 1986). However, if tree defoliation is not sufficiently severe or occurs only for a short duration, the regrowth of trees may be stimulated instead of their being killed (Lay 1965; Stuart-Hill & Tainton 1988, 1989).

The impact of browsers strongly interacts with fire; regrowth from sprouting (after fires) is often palatable and within the reach of browsers, while browsers keep woody plants within the flame zone (Scholes & Walker 1993; Trollope 1980). Trollope (1974) reported a combination of fire and heavy browsing to be successful in stopping and reversing bush encroachment and increasing grass density. Belsky (1984) showed that small browsing mammals (Grant's and Thomson's gazelle, dikdik and impala) play a significant role in containing woodland regeneration through damaging seedlings and keeping young trees at a fire-sensitive height in the Serengeti National Park. Large-sized browsers like elephant, black rhino, giraffe, eland and wildebeest also reduce and damage woody growth (Spinage & Guinness 1971; Cumming 1982; Barnes 1983; Pellew 1983; Skarpe 1991) (browsing as control measure for bush encroachment is discussed in more detail under 'Control measures').

1.8 Global Climate Change

The fact that worldwide increases in woody vegetation in savannas (Johnson et al. 1993; Scholes & Walker 1993; Kreuter et al. 1999) during the 20th century coincided with global climate change (Nielson 1986; Bazzaz 1990; Dukes & Mooney 1999) has led to the presumption that the latter might be driving bush encroachment. The different elements of climate change i.e. increased CO_2 levels and elevated temperatures, may both have an effect on savanna distribution and dynamics (Emanuel et al. 1985a,b). As a group, C_4 plant species (including most savanna grasses) have, on average, a higher photosynthetic rate than C_3 species (including most trees and shrubs) (Cresswell

et al. 1982). Thus, C_4 plants are more efficient in terms of carbon uptake in photosynthesis and growth. It has been hypothesized that as global CO_2 levels rise, those species favoured most by increased CO_2 (i.e. C_3 tree species) will be more competitive and increase in importance relative to those favoured least (i.e. C_4 grass species) (Johnson et al. 1993; Midgley et al. 1998). A study by Wand et al. (1996) did not support this hypothesis, but rather suggested that differential changes in resource use efficiency between grass and woody species, or morphological responses of grass species, could alter the competitive balance. Kramer (1981) argued that increases in photosynthesis in relation to elevated CO_2 are often only temporary, being most pronounced in seedlings or in initial stages of growth, and will not greatly affect ecosystem function and productivity. The effects of CO_2 acclimation (the capacity to adapt to elevated CO_2) by different plant species has also been viewed as a major unknown factor (Bazzaz 1990).

Global warming, on the other hand, may favour C_4 grasses more than C_3 shrub and tree species, because C_4 species generally have a higher optimum temperature for photosynthesis (Dukes & Mooney 1999). However, these authors and Moshe et al. (2000) warned against predictions simply based on plants' photosynthetic pathways or their responses in the absence of other species. In particular, extrapolations from small-scale and short-term studies must be treated with 'healthy scepticism' (Seastedt et al. 1998). Moreover, complex interactions among CO_2 effects and other factors (such as nutrients, temperature, rainfall patterns and life-forms) will affect competition among species in ways that cannot yet be predicted with confidence (Bazzaz 1990; Archer 1996; Dukes & Mooney 1999). In conclusion, research addressing interaction effects of all elements of climate change (i.e. CO_2, temperature and rainfall) and their impacts on plant communities (instead of single species) is much needed.

1.9   Overall Trends

This literature review assessed numerous studies on the factors affecting bush encroachment, with emphasis on encroachment by *Acacia* species. These studies are summarized in Table 1.1 with respect to the study area, mean annual precipitation, study species, and effects of particular factors on the tree-grass ratio. Furthermore, we evaluated the experimental design in terms of whether treatments and controls were replicated or not, in light of replication being absolutely essential to control for variation of the populations and/or systems studied in time and space (Connell 1983; Goldberg & Barton 1992). Table 1.1 facilitates comparison among the effects of particular factors and particular species, as well as assessing the generality of results. The main trends were as follows:

Grazing:-   Heavy grazing mostly increased the tree-grass ratio, whereas light/moderate grazing had the opposite or no effect.

Fire:-   Fire generally had a negative effect on juvenile and mature trees, especially when intense. Conversely, fire improved seed viability and germination.

Rainfall:-   High rainfall always benefited the tree component, except in one study where intermediate rainfall had no effect.

Nutrients:-   Among the few studies that were done, nutrient addition either had a negative or no effect on the tree-grass ratio.

Browsing:-   Results for browsing are inconsistent, but relatively few studies were considered (because browsing was not one of our experimental treatments).

Table 1.1: Summary of studies on the determinants of bush encroachment, with emphasis on *Acacia* encroachment. Abbreviations used: BE = bush encroachment, Rain = mean annual precipitation, Rep = replication, SA = South Africa, USA = United States of America.

Reference	Study area	Rain (mm)	Rep?	Species studied	Aspect studied	Effect of factor on tree/grass ratio (positive +, negative -, or no effect 0)					
						Grazing / Clipping	Fire	Rainfall	Nutrients	Browsing	Other
Belsky (1984)	Serengeti, Tanzania	830	Yes	*Acacia hockii, A. senegal*	Small trees (< 1 m)					-	
Chirara et al. (1999)	SW Zimbabwe	600	Yes	*A. karroo*	Seedling survival and growth	Germination - Growth + Survival +					
Du Toit (1972a)	Eastern Cape, SA	435	No	*A. karroo*	Tree reestablishment after eradication	Grazing exclusion 0	0				
Du Toit (1972b)	Eastern Cape, SA	435	No	*A. karroo*	Woody regrowth after clearing					-	
O'Connor (1995)	Eastern Cape, SA	759	Yes	*A. karroo*	Early recruitment	+		High +			Shade + Dung -
Stuart-Hill & Tainton (1988, 1989)	Eastern Cape, SA	422	Yes	*A. karroo*	Grass *vs* browse production	+				Moderate +	
Trollope (1974, 1980)	Eastern Cape, SA	510	No	*A. karroo*	Woody regrowth after clearing		Intense -			-	Fire & Browsing interaction -
O'Connor & Crow (2000)	Eastern Cape, SA	772	N/A	*A. karroo* inter alia	Rate/pattern of BE by aerial photography			High +			
Smit & Rethman (1992)	Northwest, SA	620	No	*A. karroo, A. nilotica, A. tortilis*	Tree *vs* grass density	Long-term light - Short-term heavy +					
Babalwa & Witkowski (1997)	Laboratory	N/A	Yes	*A. karroo, A. tortilis, Chromolaena odorata*	Seed viability under different temperatures		Species dependent				
Wand et al. (1996)	Greenhouse	N/A	Yes	*A. karroo, Themeda triandra* (grass)	Growth						Elevated CO_2 0 UV-B radiation 0
Donaldson (1967a)	Northern Cape, SA	377	Yes	*A. mellifera*	Root kill of mature trees		Intense -				
Donaldson (1967b)	Northern Cape, SA	378	Yes	*A. mellifera*	Permanent tree eradication		Intense -				

Table 1.1 (cont.)

Reference	Study area	Rain (mm)	Rep?	Species studied	Aspect studied	Effect of factor on tree/grass ratio (positive +, negative -, or no effect 0)					
						Grazing / Clipping	Fire	Rainfall	Nutrients	Browsing	Other
Joubert (1966)	Namibia	200-500	No	A. mellifera	Tree vs grass cover	+	-				
Moshe et al. (2000)	Greenhouse	N/A	Yes	A. mellifera	Production						Elevated CO$_2$: trees + grass=spp.dependent
Skarpe (1990a)	Kalahari, Botswana	300	No	A. mellifera inter alia	Mature tree density	Heavy + Moderate 0 No grazing 0					
Skarpe (1990b)	Kalahari, Botswana	300	Partly	A. mellifera inter alia	Mature tree density	+					
Hayashi (1992)	Kenya	1088	Yes	A. mellifera, A. senegal, A. tortilis	Recruitment	No grazing: Trees + Grass +					
Wilson & Witkowski (1998)	Nursery	N/A	Yes	A. nilotica, A. karroo, A. tortilis	Recruitment			Frequent +			
Knoop & Walker (1985)	Northwest, SA	630	No	A. nilotica, A. tortilis	Tree performance when grasses cleared	Grass clearing +					
Rohner & Ward (1999)	Negev desert, Israel	<25	Yes	A. raddiana, A. tortilis	Germination and seedling survival			High +			Seed ingestion by herbivores +
Cohn et al. (1989)	Greenhouse	N/A	Yes	A. smallii	Competition between tree seedlings & grass				-		
Van Auken et al. (1985)	Greenhouse	N/A	Yes	A. smallii	Seedling growth (no grass in exp.)				0		
Smith & Shackleton (1988)	Growth chambers	630	N/A	A. tortilis	Germination, establishment & biomass						Shade: germination + establishment - biomass -
Caldwell et al. (1987)	W North-America		Yes	Artemisia tridentata	Immediate P-competition with grasses	+					
Harrington (1991)	Australia, Semi-arid grasslands	330	Yes	Dodonaea attenuata	Shrub recruitment			High +			
Strang (1974)	Zimbabwe	750 - 1100	Yes	Julbernardia globiflora, Brachystegia spiciformis	Woodland succession	Long-term -	-			Seeds destroyed	

Table 1.1 (cont.)

Reference	Study area	Rain (mm)	Rep?	Species studied	Aspect studied	Effect of factor on tree/grass ratio (positive +, negative -, or no effect 0)					
						Grazing / Clipping	Fire	Rainfall	Nutrients	Browsing	Other
Archer (1989)	Texas, USA	680	N/A	*Prosopis glandulosa*	History of BE by aerial photography	Heavy +		High +			
Brown & Archer (1987)	Texas, USA	680	Yes	*P. glandulosa*	Seed disperal; Seedling density						Seed dispersal by cattle +
Brown & Archer (1989)	Texas, USA	990	Yes	*P. glandulosa*	Germination & survival	Germination + Survival 0					Dung -
Brown & Archer (1999)	Texas, USA	721	Yes	*P. glandulosa*	Seedling germination, growth, survival	0		High 0			
Bush & Van Auken (1990)	Texas, USA	720	Shade:Yes Clipping: No	*P. glandulosa*	Germination, growth	+					Shade -
Bush & Van Auken (1995)	Texas, USA	720	Yes	*P. glandulosa*	Seedling growth	+					
Johnson *et al.* (1993)	Growth chamber	N/A	Yes	*P. glandulosa*	Tree seedling growth						Elevated CO_2 +
Van Auken & Bush (1989)	Greenhouse	N/A	Yes	*P. glandulosa*	Seedling growth	+			-		
Weltzin *et al.* (1997)	Texas, USA	682	Yes	*P. glandulosa*	Woody plant establishment					-	
Anderson *et al.* (2001)	Texas, USA	734	Yes	*P. glandulosa, Juniperus ashei*	Seedling survival and growth						Shade: survival +, growth 0
Pitt *et al.* (1998)	British Columbia, Canada	355	Yes	*Pinus contorta*	Seedling damage	Trampling -					
Schultz *et al.* (1955)	California, USA	813	Pseudo	Various	Germination		+				Dense grass -
Bradstock & Auld (1995)	Close to Sydney, Australia		No	Various	Tree germination (seed viability)		+				
Jeltsch *et al.* (1996)	Kalahari, SA & Botswana	220-385	Model	Various	Coexistence of trees & grass	Heavy + Intermediate 0	Intermediate 0	Intermediate 0			
Jeltsch *et al.* (1997)	Kalahari, SA & Botswana	220-385	Model	Various	Currently recommended stocking rates	20 years 0 100 years +					
Shackleton (2000)	Mpumalanga, SA		Yes	Various	Germination of surface seed		-				

1.10   Tree Influence on the Understory

Trees are of considerable importance for the biodiversity and productivity of savannas and their function may vary with their population structure, density and distribution (Jeltsch *et al.* 1996). Trees growing at low density in arid and semi-arid pastoral ecosystems have often been found to alter their understory environments. Compared to neighbouring grasslands, soils beneath tree canopies have higher concentrations of microbes, organic matter, mineralizable nitrogen, extractable phosphorus, potassium and calcium, better soil structure, improved water infiltration, reduced temperatures and reduced evapotranspiration (Tiedemann & Klemmedson 1977; Kellman 1979; Hobbs & Mooney 1986; Walker & Knoop 1987; Palmer *et al.* 1988; Frost & McDougald 1989; Belsky *et al.* 1989, 1993b,c; Belsky 1994; Smit & Swart 1994; Barnes & Archer 1996; Jarvel & O'Connor 2000; Munzbergova & Ward 2001). The higher nutrient contents of subcanopy soils are ascribed to bird and mammal droppings (Dean *et al.* 1999), leachate through fall and litter (Teague & Smit 1992), nutrient accumulation at the trunk base through stem flow and bark sloughing (Kellman 1979; Potter 1992; Belsky *et al.* 1993b), and hydraulic lift whereby trees act as nutrient pumps (Bosch & Van Wyk 1970) that draw soil minerals from deep underground and bring them to shallower soil layers. In addition, the beneficial effects of shade on plant nutrient uptake may increase subcanopy plant growth (Eriksen & Whitney 1981; Samarakoon *et al.* 1990).

The negative influences of trees on their understories comprise rainfall interception (Stuart-Hill *et al.* 1987), reductions in solar radiation (Belsky *et al.* 1989, 1993b), enhanced soil salinity (Munzbergova & Ward 2001), lower pH (Belsky *et al.* 1989) and competition between trees and grass for water and nutrients may adversely affect understory grasses (Dye & Spear 1982; Walker & Noy-Meir 1982; Stuart-Hill *et al.* 1987). Soil moisture does not necessarily differ between the canopy and grassland zones, because moisture lost through interception of rainfall may be ameliorated by hydraulic lift (see 'Rainfall'), better water infiltration, improved soil water-holding capacity, reduced temperatures and lower evapotranspiration (due to shading and more plant litter). Belsky *et al.* (1993b) showed that, although there were seasonal differences, there was no difference in soil moisture between the two zones at any depth when analysed over the entire year. Some studies show that inter-tree open grasslands tend to be more patchy and species-rich (Hobbs & Mooney 1986; Belsky *et al.* 1989) relative to the under-canopy vegetation, although the converse has also been reported (Munzbergova & Ward 2001). Such modification of grass species composition is usually strictly limited to the canopy zone and may be accounted for by altered light, soil moisture and nutrient conditions and possibly allelopathy (Hobbs & Mooney 1986; Munzbergova & Ward 2001). Stuart-Hill *et al.* (1987) showed that there is a specific pattern of

subcanopy grass production related to the angle of incidence of radiation and precipitation. To summarize the effects of trees on grass production, the latter declines with:

(1) an increase in tree size (Stuart-Hill & Tainton 1988, 1989);

(2) an increase in tree density beyond a critical level (Aucamp *et al.* 1983; Billé 1985; Hobbs & Mooney 1986; Stuart-Hill *et al.* 1987; Stuart-Hill & Tainton 1989; Smit & Swart 1994; Smit & Rethman 2000);

(3) complete removal of trees – supported by Stuart-Hill *et al.* (1987) and Stuart-Hill and Tainton (1989) but not by Du Toit (1968); and

(4) frequent (moderate) tree defoliation due to increased competitiveness of trees (Stuart-Hill & Tainton 1988, 1989).

Competition within the woody component of the community plays an important role in the spacing pattern of savanna trees, depicted by a positive correlation between distance to the nearest neighbour and combined size (Smith & Goodman 1986; Wiegand *et al.* 2000b). Facilitation, on the other hand, can result in the aggregation of woody individuals, causing a typically clumped distribution (Archer *et al.* 1988). Aggregated trees protect one another and new recruits under their canopies from fire. This is because herbaceous production is suppressed in the bushclump zone (Jarvel & O'Connor 2000) resulting in lower fuel loads and consequently, less frequent and cooler fires (see 'Fire'). Trees can also serve as recruitment foci for bird- and ungulate-dispersed seeds of the same or other tree/shrub species (Archer *et al.* 1988), because trees are focal points for animal activity through supplying nest sites, shade and scarce food resources (Pianka & Huey 1971; Belsky 1994; Dean *et al.* 1999). The alteration of microclimatic and edaphic properties (as described above) in these tree clumps may further promote germination and establishment of tree seedlings. These processes are self-reinforcing and as new clusters are initiated and existing clusters expand, coalescence to continuous canopy woodlands may eventually occur (Archer 1989).

1.11 Tree Recruitment (Dispersal, Germination & Establishment)

Range expansion or encroachment of a woody species requires successful dispersal, germination and seedling establishment (O'Connor 1995). There are three mechanisms that can improve the local recruitment probability of tree seedlings: (1) localized increase in seed density; (2) reduced competition with grasses; and (3) improved resource conditions. In a modelling approach, Jeltsch *et al.* (1998) showed that small-scale heterogeneities may favour the establishment of tree seedlings either by reducing competition with grasses (e.g. vegetation clearing due to colonial

rodents or aardvark (*Orycteropus afer*) diggings) or by increasing the number of opportunities for establishment (e.g. clumped seed distribution in dung or due to fossorial rodents). The question of whether or not recruitment is seed-limited is a fundamental issue in plant population dynamics (e.g. Ackerman *et al.* 1996; Crawley & Rees 1996). Recruitment may also vary between years, e.g. recruitment may be seed-limited in peak years (under optimal climatic conditions) but predator-limited in less favourable years (Crawley & Rees 1996). In stark contrast with the rapid recorded rates of woody invasion, rates of restoration of palatable grasses to degraded rangelands are limited by seed availability and short seed dispersal distances, and recovery times may exceed 70 years (Donaldson & Kelk 1970; O'Connor 1991).

A number of studies suggested that increased and effective tree seed dissemination by cattle (Scott 1967; Walker *et al.* 1981; Archer 1989; Brown & Archer 1989; Schultka & Cornelius 1997) alleviated seed-limitation that restricted tree recruitment prior to introduction of domestic livestock. Some of the positive effects that ingestion by herbivores may have on tree seed germination are:

(1) removal of shade-intolerant seeds from parent plants;

(2) reduction of the time that seeds are exposed to predation or rainfall moisture (causing seed to swell and then shrivel);

(3) destruction of seed predators, e.g. bruchid beetle eggs and larvae in the pods; and

(4) abrasion of hard seed coats (Brown & Archer 1987; Hoffman *et al.* 1989; Miller & Coe 1993; Tybirk *et al.* 1993; Rohner & Ward 1999). However, seeds may also be destroyed (digested) during passage through the alimentary canal of ungulates, e.g. Tybirk *et al.* (1993) found a 98 % loss of *Acacia* seeds due to ungulate digestion. With *A. mellifera* in particular, Donaldson (1967a) showed that when undamaged seed were fed to steers, only 10 % of the seed were recovered in the faeces, of which only 30 % germinated in the laboratory (giving a total of 3 %).

Contrary to the conventional wisdom that cattle dung is a favourable medium for seed germination (e.g. Schultka & Cornelius 1997), emergence of *Prosopis glandulosa* seeds from dung was lower than that of bare seed placements (Brown & Archer 1989), whereas not a single *Acacia karroo* seedling emerged from 660 undamaged seeds placed in cattle dung (O'Connor 1995). This may be the result of increased predation by rodents attracted to dung (Janzen 1982), desiccation due to the dark colour of the dung (Brown & Archer 1989; Wilson & Witkowski 1998), or high nitrogen in dung pats that may have adverse effects on seedling establishment (Wickens 1969).

Competition from the herbaceous layer has been widely assumed to be one of the principal mechanisms underlying the resistance of intact communities to invasion by trees, e.g. in the cases of *A. nilotica*, *A. tortilis* (Knoop & Walker 1985) and *P. glandulosa* (Bush & Van Auken 1990).

However, seedling establishment can also be enhanced by low-growing species, particularly in physically stressful sites (Tielbörger & Kadmon 2000). Even though competition may be the more likely event, the net effects of established vegetation on tree seedling growth and survival will be a trade-off between competition and facilitation (Callaway & Walker 1997; Holmgren *et al.* 1997; Tielbörger & Kadmon 2000). Tree seedling establishment may also be constrained by other factors such as drought, fire (Medina & Silva 1990), shading (Smith & Shackleton 1988; Bush & Van Auken 1990) and herbivory (Springuel *et al.* 1995; Weltzin *et al.* 1997), but it is often difficult (if not impossible) to separate the effects of these factors from the effects of herbaceous competition.

Berkowitz *et al.* (1995) showed that the intensity of competition between tree seedlings and herbaceous vegetation might not be related either to community type or the biomass of the intact community. Instead, variation in the intensity of competition can be related to the underlying favorability of the site for the growth of a particular tree species, with more intense competition as the site quality increases. These authors also clearly differentiate between intensity and duration of competition: differences among early successional communities in resistance to tree seedling establishment may be caused by variation in the duration of competition resulting from differences in height and canopy structure of the herbaceous communities, rather than by the intensity of the competitive effects. A good example comes from O'Connor (1995) where the first year of *A. karroo* seedling establishment was not influenced by competition, although he suggested that competition from the grass sward may assume greater importance in subsequent years for seedlings that are already established.

As mentioned, shading can inhibit tree seedling establishment (Smith & Shackleton 1988; Bush & Van Auken 1990). In general, both African and Australian *Acacias* are thought to be canopy/shade intolerant (Roux & Middlemiss 1963; Obeid & Seif El Din 1970; Milton 1980) and that removal of seeds from parent plants is one of the benefits of mammalian dispersal (Tybirk *et al.* 1993). Smith and Taylor (unpubl. *op.cit.* Smith & Goodman 1986) showed reduced root and shoot biomass of *A. tortilis* seedlings due to shading. However, shading of *A. karroo* seeds resulted in higher germination and seedling survival, attributed to more favourable soil moisture conditions (O'Connor 1995). *A. mellifera* (Kraaij *pers. obs.*) and *A. raddiana* (Springuel *et al.* 1995) seedlings also readily occur under parent trees. Contrastingly, it was noted that *A. mellifera*, *A. tortilis* and *A. nilotica* seedlings/juveniles generally occur in the area around the mother plant, but not underneath the crown spread of the latter (Donaldson 1967a; Smith & Goodman 1986; Smith & Shackleton 1988). This phenomenon leads to the characteristic type of propagation in the form of clumps/thickets (Wiegand *et al.* 2000d).

1.12   Equilibrium Models

The evidence from different studies and opinions about equilibrium and stability of savanna systems are quite opposing and divergent. In addition, stability is a complex concept that includes both functional and species stability (Roberts 1985). The widespread and persistent occurrence of savannas (tree-grass coexistence) suggests some form of stability, whereas the phenomenon of bush-encroachment suggests semi-stability (because woody thickets may take decades to revert to open savanna, if it ever does). Contrastingly, the asymmetry of the competitive effect of trees on grass *vs* grass on trees implies instability (Scholes & Archer 1997). The major opinions are presented below:

(1) The traditional view was that of a *tree-grass co-dominance* in a *competitive equilibrium* as predicted by Walter's (1971) two-layer hypothesis (see 'Rainfall'). The assumption is that a form of balanced competition would result if mature trees could outcompete grasses, but grasses could outcompete establishing trees (Scholes & Archer 1997), mainly based on rooting niche separation. However, a stable tree-grass coexistence may only be possible under very specific conditions (Jeltsch *et al.* 1996), e.g. on finer textured soils where grasses are favoured by water retention in the upper soil layers (Noy-Meir & Walker 1986), or when water is translocated by tree roots to shallower soil layers (i.e. hydraulic lift, Caldwell & Richards 1989).

(2) Unlike the classical view of tree-grass co-dominance in a competitive equilibrium, Scholes and Walker (1993) proposed in their '*multi-dimensional asymmetric*' model that the interactions between established trees and grasses are strongly asymmetrical, with trees having a much larger effect on grasses (partly through their ability to shade grass) than *vice versa*. Therefore, the tree-grass mixture doesn't represent a competitive balance, but has an inherent tendency to become woodier. This trend is periodically offset by fires, and is limited at the upper end by tree-on-tree competition. The tree-grass ratio is determined more by the recent history of episodic establishment and mortality events relating to the woody plants than by competitive interactions between trees and grass. The asymmetry in competition between tree seedlings and grasses, on the other hand, is in favour of the grasses. When the grass layer is reduced by heavy and continuous grazing, tree seedlings can grow beyond the control of grass competition and fire, and the result is bush encroachment. This model shows some similarities with the view that *cycling* occurs between different steady states (i.e. woody vegetation alone or high herbaceous biomass with little woody vegetation). The transition between states is ascribed to natural, large-scale oscillations, involving fire, browsers, grazers and competition for soil water (Norton-Griffiths 1979; Walker *et al.* 1981). This model also corresponds with the *non-equilibrium* view that suggests that the coexistence of trees and grasses is achieved through disturbances (Skarpe 1992; Scholes &

Walker 1993). Similarly, the view of savannas as *patch-dynamic* systems (Skarpe 1992; Scholes & Archer 1997; Wiegand *et al.* 2000b) is based on stochastic disturbances (e.g. fire, extreme rainfall/drought) and variability of many factors (soil properties, rainfall, fire, herbivory) in time and space, with emphasis on variation among patches. Savannas, as patch-dynamic systems, will comprise of patches of almost pure grassland, patches of parkland and patches of woodland (i.e. 'natural bush encroachment'), as well as intermediary stages.

(3) A third view proposed that succession is *linear* and *irreversible* from one state (grassland) to another (woodland) and not a cyclical replacement series (Archer *et al.* 1988). The fact that spontaneous reversions to grassland have rarely been observed may be an artefact of the longevity of trees (Scholes & Archer 1997). A *threshold* (e.g. a grazing threshold) may also exist between different steady states (as in so-called 'state-and-transition' models, Jeltsch *et al.* 1997), instead of a linear process. If grazing pressure is maintained (with the natural consequence of reduced fire frequency and intensity) and woody plants begin to establish, a transitional threshold is eventually reached. Autogenic modification of soils and microclimate by invading shrubs follows and, over time, a stable shrubland or woodland system may develop. The modification of soil, seed bank and vegetative regeneration potential makes it unlikely that this new assemblage will revert to grassland, even following a curtailment of grazing (Archer 1989).

(4) Other authors are of the opinion that *stable equilibria* are *not achievable* in many pastoral ecosystems because ecosystem dynamics are often dominated by stochastic perturbations (e.g. droughts, fire) (Ellis & Swift 1988). Equilibrium models are further problematic in that they assume density-dependent growth (which often cannot be tested), and cannot be extrapolated to the small spatial scales on which observations are often made (DeAngelis & Waterhouse 1987). Therefore, stable equilibria may be perceived over sufficiently large landscapes, though as an asymptotic limit of increasing size, not as an intrinsic property of the system.

In the end, all assessments of stability and equilibrium may be typically artefacts of the spatial and temporal scale at which we observe (Connell & Sousa 1983; DeAngelis & Waterhouse 1987; Menaut *et al.* 1990). Lack of historical/spatial perspective on short-term/small-scale studies can produce misleading conclusions (Magnuson 1990; Swanson & Sparks 1990). On a sufficiently small-scale, in space or in time, all ecosystems are unstable and transient (Watt 1947), while small-scale/short-term disequilibria may promote large-scale/long-term dynamic equilibrium or persistence (DeAngelis & Waterhouse 1987; Ellis & Swift 1988). In other words, what is an external constraint on one scale may be an interactive component of the ecosystem on a larger scale (Skarpe 1992). This concept is represented by the patch-dynamic approach (Wiegand *et al.*

2000b), whereafter savannas can be stable and persistent at a landscape scale, because the landscape consists of many patches in different states of transition between grassy and woody dominance (Scoles & Archer 1997). Lastly, the concepts of stability, stochasticity and equilibrium/non-equilibrium need be clearly defined in relation to one another. As Illius and O'Connor (1999) pointed out: "virtually all natural systems are to some extent non-equilibrial, if by this is meant that environmental fluctuations and stochastic variation are constantly redefining the equilibrium point".

1.13 Control Measures

The harmful effect of bush competition on grass production is very evident, particularly during seasons with low rainfall (Du Toit 1972a). Du Toit found that grass production in veld cleared of *A. karroo* outyielded uncleared veld by 64 %. Similarly, in an area close to the study site with the same vegetation type (i.e. Kimberley Thorn Bushveld, Low & Rebelo 1998) hay yields exponentially decreased with an increase in *A. mellifera* density (Donaldson & Kelk 1970). Gammon (1983) reported a two- to three-fold increase in carrying capacity for cattle following bush clearing in the south-western lowveld of Zimbabwe. From a rancher's point of view, bush clearing should be profitable if revenue from increased livestock/game production (as a result of increased grass production) exceed the cost of clearing. However, it is generally deemed unlikely that bush eradication can be economically applied on a large scale in areas with a relatively low livestock carrying capacity, and cost of clearing often exceeds the value of the land (Donaldson 1967a).

In the agricultural sphere, there are two alternatives to the control of bush encroachment. The first is to adapt the vegetation to the animal factor or secondly, to adapt the animal factor to the vegetation. The general approach among farmers used to be the former, involving control of bush encroachment through various means, i.e. mechanical (Donaldson 1966, 1978; Gammon 1983), chemical (Scott 1967), burning (Joubert 1966), and combinations of these (Trollope 1974, 1980). The second alternative of adapting the animal factor to the vegetation involves introducing a browsing animal to a conventional cattle ranching system. Of all control measures, only browsing will be discussed, because browsing (≈herbivory) is one of the main factors affecting tree-grass dynamics (see above).

The use of a browsing animal in combating bush encroachment requires that the bush is palatable and at an available height to the browsing animal. The use of browsing for manipulating the tree-grass ratio is particularly suitable for the arid savannas, because it is only in these areas that a

significant proportion of the bush species is acceptable to goats (Trollope 1980). Goats are preferential browsers on woody plants and forbs (Grunow 1980; Cooper 1982) and have anatomical and physiological adaptations that assist in efficient utilization of poor quality forage e.g. mobile lips, good chewing ability, high saliva production, microbial efficiency, large rumen and slow rate of passage through the gut (Maher 1945; Owen-Smith 1993). Moreover, they have the ability to adapt their forage preferences (Du Toit 1972b) and show large seasonal variations in their feeding patterns (Cooper 1982). In short, goats have a wider grazing spectrum than sheep, cattle and some game species, that results in far broader, less selective utilization of the vegetation, thereby benefiting the general level of productivity besides contributing to the control of woody plants (Campbell *et al.* 1962; Du Toit 1972b; Owen-Smith & Cooper 1985). They defoliate bush severely and damage plants especially when biting off whole shoots (Du Toit 1972b; Cooper 1982). As a consequence, continuous browsing by goats restricts bush competition and improves grass cover, composition and vigour (Du Toit 1972b; Fierro *et al.* 1986; Teague 1986). However, if tree defoliation is not sufficiently severe or occurs only for a short duration, the regrowth of trees may be stimulated instead of their being killed (Lay 1965; Stuart-Hill & Tainton 1988, 1989). Goat enterprises were shown to be economically viable in the Eastern Cape (Aucamp *et al.* 1981) and semi-arid Australia (Condon 1986b) where the goats opened up heavily scrub-infested rangelands that were rendered useless for sheep and cattle grazing. In addition, the goats proved to be easier to manage and more resistant to disease and parasites than sheep (Condon 1986b).

Guidelines for the control of bush encroachment have existed for a long time, but the long-term ecological consequences of bush clearing have more recently come under the spotlight (Hoffman *et al.* 1999). Removal of encroaching bush should not be contemplated without due consideration of what will replace them, taking soils, seed banks and vegetative regeneration potentials into account (Pakeman & Hay 1996; Low *et al.* 1999). It is highly unlikely that the desirable, late successional grass species will again become dominant components of the vegetation within a reasonable period of time (Booth 1941; Joubert 1966; Roux 1969; Donaldson & Kelk 1970). O'Connor (1991) ascribed the proneness to extinction (and extremely slow reestablishment) of many perennial sublimax/climax grasses to certain life-history attributes *viz.* long life expectancy, small reproductive efforts in few, large propagules, and short-lived seeds (so-called *K*-selected species). Donaldson and Kelk (1970) reported an increase in herbage production following *A. mellifera* eradication that was related to an increase in the number and size of the pioneer and subclimax grass species, without any change in species composition – a lack of suitable seed supply of climax species being one of the limiting factors. In addition, regeneration of trees from seed reserves in the soil can be expected for several years after eradication, with a strong correlation between the density of the

original stand and the level of regeneration (Du Toit 1972a). Consequently, the necessity of follow-up treatments after initial eradication adds to the high cost of bush control.

1.14 Conclusions

Despite the fact that both savannas and bush encroachment have been intensively studied, it is clear that there is much controversy about the mechanisms underlying tree-grass dynamics and the causes of bush encroachment. Especially for bush encroachment, the poor results of bush control measures show that this economically important phenomenon is poorly understood (Teague & Smit 1992; Jeltsch *et al.* 1997; Weltzin *et al.* 1997), and that alternative theories are needed to explain tree-grass coexistence in savannas (Higgins *et al.* 2000). Many levels of interaction occur between the various biotic and abiotic determinants of savanna structure, encompassing competition and facilitation, acting differentially on trees and grass and patchily in time and space. Although it is essential to continue the search for general rules/trends applicable to savanna systems, it may be inappropriate to try and find a universal cause of bush encroachment. The complexity and variation of the environmental factors involved in savanna dynamics, in addition to divergent management histories, often make generalizations and extrapolations across (even similar) areas invalid.

In order to improve our understanding of savannas, and formulate lucid and effective guidelines for managing bush encroachment, research will have to be at an appropriate scale – taking the detail of the particular system into account, but not losing sight of the overall picture (Wiegand *et al.* 2000b). On this point, the patch-dynamic approach may be particularly useful by regarding bush encroachment as a natural part of a heterogenous and dynamic system. Accordingly, management should aim to contain bush encroachment to its natural level that is appropriate to the scale of the patchiness of the system (Wiegand *et al.* 2000b). This will involve finding trade-offs between short-term disadvantages (reduced grass biomass) and long-term advantages (increased soil nutrient levels) of an increased tree-grass ratio.

2. EFFECTS OF RAIN, NITROGEN, FIRE AND GRAZING ON TREE RECRUITMENT AND EARLY SURVIVAL

2.1 Abstract

Moisture, nutrients, fire and herbivory are the principal factors governing tree-grass ratios of savannas. We investigated tree (*Acacia mellifera*) recruitment after fire and under conditions of maximum-recorded rainfall, nitrogen addition and grazing in a completely-crossed field experiment. We employed a similar garden experiment, but excluding fire. Tree germination in the field was extremely low, probably due to below-average natural rainfall in plots that only received natural rain, and insufficient watering frequency in irrigated plots. Due to low germination in the field experiment, no treatment significantly affected tree recruitment. Frequent watering, no nitrogen addition and grass clipping enhanced tree recruitment in the garden experiment, with significant interactions between rain, nitrogen and grazing. We infer that above-average rainfall years with frequent rainfall events are required for mass tree recruitment. Grass defoliation makes space and resources available for tree seedlings. Nitrogen enrichment increases the competitive ability of fast-growing grasses relatively more than that of the N_2-fixing tree component. Contrary to conventional wisdom that grazing alone causes encroachment, we suggest that there are complex interactions between the above mentioned factors and 'triggering' events such as unusually high rainfall.

Keywords: Tree-grass competition, *Acacia mellifera*, rainfall frequency, soil nitrogen, interaction effects.

2.2 Introduction

The encroachment of woody plants in grasslands and savannas (termed 'bush encroachment') is well known and is globally a widespread phenomenon (Johnson *et al.* 1993, Kreuter *et al.* 1999). The encroaching species are often unpalatable to domestic livestock because of their chemical and/or physical defences (Rohner & Ward 1997). Consequently, bush encroachment reduces carrying capacity for grazing animals (Joubert 1966; Dean & Macdonald 1994), thereby threatening the livelihood of commercial and communal game and livestock ranchers (Condon 1986a). Bush encroachment is of serious socio-economic concern in arid and semi-arid regions, such as southern Africa, where other forms of agriculture are not feasible on account of the low rainfall.

The problem of bush encroachment is particularly acute in the communal rangelands of South Africa where human and livestock population densities are very high and consequently heavy grazing (which is often considered to lead to bush encroachment) is common (Walker *et al.* 1981). In South Africa alone, 13 million hectares were already affected by bush encroachment in the 1960s (Van der Schijff 1964) and it is considered to be far higher today. It is not only the extent of woody encroachment, but also the rate at which it occurs, that is of great concern. Van Vegten (1983) described a tripling of total woody biomass in eastern Botswana within 25 years, while Hoffman and O'Connor (1999) measured a tripling of woody cover in KwaZulu-Natal in 43 years. Dean and Macdonald (1994) provide evidence that the production potential of drylands has decreased markedly throughout the savanna and karoo biomes of the Cape Province (South Africa). The agricultural loss in southern Africa due to bush encroachment was quantified in terms of substantial seasonal grass yield reductions, e.g. 32 – 40 % in Zimbabwe (Dye & Spear 1982) and 41 % in the Eastern Cape (Du Toit 1972b).

From an ecological perspective, bush encroachment may be seen as a natural process involving competition between the tree and grass component of savannas (Fowler 1982; Davis *et al.* 1998), and being only a particular stable/unstable state in plant succession (Walker *et al.* 1981; Frost *et al.* 1985; Noy-Meir & Walker 1986). Two main mechanisms have been proposed to be responsible for long-term coexistence of plant populations, *viz.* functional/physical niche differentiation; and heterogeneity (spatial- and temporal variation) of the environment (Walter 1971; Berendse 1979; Fowler 1982). The major factors driving savanna dynamics and functioning are rainfall, nutrients, fire and herbivory (Schultz *et al.* 1955; Frost *et al.* 1985; Knoop & Walker 1985; Van Auken *et al.* 1985; Walker & Knoop 1987; Stuart-Hill & Tainton 1988, 1989; Teague & Smit 1992; Jeltsch *et al.* 1996; Van Wilgen & Scholes 1997; Higgins *et al.* 2000). The interaction of these driving forces consequently determines the tree-grass ratio, and ultimately the occurrence/absence of bush encroachment (Van der Schijff 1964).

The effects of most factors affecting tree-grass dynamics (grazing, browsing, fire, nutrients, soil moisture) are generally explained in terms of an alteration in the competitive ability of grasses *vs* trees in acquiring resources (Walter 1971; Walker *et al.* 1981; Fowler 1982; Frost *et al.* 1985; Stuart-Hill & Tainton 1988; Cohn *et al.* 1989; Davis *et al.* 1998). This explanation is largely based on the two-layer model of savanna dynamics proposed by Walter (1971). Walter hypothesized that grasses are the superior competitors for water (and nutrients) in the upper soil layers, while trees monopolize the deeper soil resources. It follows that if grasses are removed, e.g. by heavy grazing or fire, grass roots extract less water from the topsoil, allowing more water to percolate into the subsoil, where it is available for woody growth. However, this model has been shown to be an

over-simplification (Teague & Smit 1992) and often inappropriate, e.g. in areas where shallow soil layers do not allow stratification of grass and tree roots and yet there is bush encroachment (Noy-Meir & Walker 1986; Ward 2000, 2001; Wiegand *et al.* 2000c).

Grazing:- Although this is the most frequently-cited cause of bush encroachment (Joubert 1966; Madany & West 1983; Van Vegten 1983; McPherson & Wright 1990; Skarpe 1990a,b; Smit & Rethman 1992; Perkins & Thomas 1993; Schultka & Cornelius 1997), and often considered to be a prerequisite, studies on the effects of grazing on bush encroachment generally produced inconsistent results (*cf.* Andersson 1856; Du Toit 1972a; Strang 1974; Brown & Archer 1989, 1999; Scholes & Walker 1993). Grazing may have a similar effect to fire by creating gaps and making below- and above-ground resources (i.e. water, nutrients, light) available for tree seedlings to establish (Bush & Van Auken 1995; Jeltsch *et al.* 1996, 1997, 1998).

Fire:- The negative impact of fire on established tree seedlings is well recognized in the literature (e.g. Du Toit 1972a; Trollope 1974, 1980; Lacey *et al.* 1982; Roberts 1986). However, the beneficial effect of burning in reducing above-ground grass biomass (and therefore competition with tree seedlings) means that fires may enhance woody recruitment (Schultz *et al.* 1955). Depending on the tree species and fire intensity, burning may also either facilitate germination by breaking seed dormancy, or prevent germination by destroying tree seeds with softer seed coats (Bradstock & Auld 1995; Babalwa & Witkowski 1997).

Soil Nutrients:- The N_2-fixing ability of leguminous trees and shrubs (including the genus *Acacia*) greatly contribute to their success in poor environments (Roux & Middlemiss 1963; Milton 1980; Van Auken *et al.* 1985; Dart *et al.* 1991). In addition, tree seedlings are almost completely dependent on cotyledons for their nutrient requirements during the first weeks of establishment (Ernst 1988). Thus, nitrogen should be more limiting to the fast-growing grasses than to these trees. We predict that an increase in soil nitrogen will enhance growth of herbaceous plants, which will then increase their negative effects on the early growth and establishment of tree seedlings (Moshe *et al.* 2000) of N_2-fixing species. If this prediction holds true, low-nutrient environments should be more prone to bush encroachment (at least by N_2-fixing tree species) than richer environments.

Rainfall:- The importance of rainfall for tree-grass dynamics is clear, it being fundamental to Walter's (1971) two-layer hypothesis (see above), which dominates the literature on tree-grass interaction in savannas. Different approaches have been adopted to examine the effects of rainfall/soil moisture on bush encroachment: several studies investigated competitive interactions

between trees and grass by manipulating and/or measuring water supply/uptake of the different components (Knoop & Walker 1985; Noy-Meir & Walker 1986), some determined rainfall requirements for tree establishment/dominance of certain species (Wilson & Witkowski 1998), whereas others tried to correlate climatic records with historical increases in woody density (Condon 1986a; Harrington & Hodgkinson 1986; Archer 1989). The latter showed that initiation and/or intensification of bush encroachment has often been associated with consecutive above-average rainfall years.

We hypothesize that:

(1) extreme rainfall is critical for mass tree seedling recruitment, which will ultimately result in bush encroachment if subsequent conditions (e.g. post-germination rainfall and fire exclusion) are also favourable to the tree component.

In addition, woody seedlings are expected to fare better under conditions of reduced grass competition (e.g. Booth 1986). Therefore, we further hypothesize that early tree recruitment will be:

(2) enhanced by pre-emergence fires;

(3) enhanced by heavy grazing; and

(4) depressed by nitrogen addition.

We tested these predictions by means of a field and a garden experiment, both investigating the effects of rainfall, nitrogen, grazing and fire (the latter was excluded from the garden experiment) and their interactions on the initial stages of bush encroachment (i.e. germination and early survival).

We used *Acacia mellifera* (Vahl) Benth. subsp. *detinens* (Burch) Brenan (Palgrave 1977; Smit 1999) [syn. *Acacia detinens* (Burch.) Brenan] as a model bush-encroaching species in these experiments because it is one of the dominant species encroaching upon vast tracts of semi-arid land in southern Africa (Becker, undated; Donaldson 1966, 1967a; Scott 1967; Donaldson & Kelk 1970; Kelk & Donaldson 1970; Palmer & Pitman 1972; Hoffman *et al.* 1999). In this study, our objectives were to investigate early recruitment of *Acacia mellifera* (the dominant invading bush in the study area, north of Kimberley, Northern Cape, South Africa) after fire and under conditions of extreme rainfall, nitrogen addition and heavy grazing. To address some of the above shortcomings, this study focused on identifying the factors and/or combinations thereof, that create ideal conditions for the initial stages of bush encroachment (i.e. 'triggering' events). We regarded tree recruitment (early establishment) as the most influencial process in the course of bush encroachment and neglected post-establishment dynamics in our study on account of the following:

(1) inevitably, germination and seedling establishment are prerequisites for an increase in tree abundance;

(2) stands of trees/bush often comprise of discrete cohorts, suggesting the importance of infrequent and large-scale recruitment events (Donaldson 1967a; Booth 1986; Condon 1986a; Harrington & Hodgkinson 1986; Skarpe 1990b; Wiegand *et al.* 2000a). Especially in the case of long-lived species, such as savanna trees, population size frequency distributions often largely reflect recruitment events, while environmental variation has little influence on post-establishment survival (Wiegand *et al.* 2000a);

(3) generally, under ranching conditions in dry areas, fires (if at all possible) are not sufficiently frequent and intense to have a significant and lasting destructive effect on mature trees (Du Toit 1972a; Trollope 1982; Higgins *et al.* 2000); and similarly

(4) browsing is unlikely to have significant negative effects on established trees as browsers are often absent from ranches or alternatively, browsing intensity is too low to affect tree survival (Lay 1965; Stuart-Hill & Tainton 1988, 1989).

2.3   Materials & Methods

Field Experiment

The study was conducted at three different sites on Pniel Estates near Barkly West (35 km north west of the city of Kimberley, Northern Cape, South Africa. The three sites were referred to as site A (28°36'11" S, 24°29'00" E; 1130 m a.s.l.), site B (28°36'11" S, 24°24'16" E; 1160 m a.s.l.) and site C (28°35'31" S, 24°22'45" E; 1150 m a.s.l.). The land used to be heavily grazed by various livestock, but since 1960, it has been moderately grazed by cattle in a multi-camp (rotational) system. The study period covered one growing season (October 2000 – April 2001). The mean annual rainfall (based on 84 records, kept since 1884) for Barkly West is 388 mm and it is extremely variable (C.V. = 39 %). Mean monthly minimum/maximum temperatures for Kimberley range between 3.2/18.2 °C in June and 17.9/32.8 °C in February with an average of 22 days of frost per year. The soil consists of nutrient-poor Kalahari sand of aeolian and local origin (Bosch 1993), varying from deep red and yellow sands to shallow and stony (Bezuidenhout 1994, 1995).

The vegetation type is semi-arid savanna, known as Kimberley Thorn Bushveld (Low & Rebelo 1998) or Kalahari Thornveld (veld type 16, Acocks 1988). There are scattered trees, mostly *Acacia erioloba* E. Mey. and *A. tortilis* (Forsk.) Hayne subsp. *heteracantha* (Burch.) Brenan while the shrub/low tree layer is dominated by *A. mellifera* (the main encroaching tree), *Grewia flava* DC. and *Tarchonanthus camphoratus* L. [*T. minor* Less.] (Palgrave 1977; Smit 1999). The herbaceous

sward mainly consists of tufted perennial grasses, the most common species being *Eragrostis lehmanniana* Nees, *Schmidtia pappophoroides* Steud., *Stipagrostis uniplumis* (Licht.) De Winter and *Aristida canescens* Henr. (in order of decreasing abundance). The following grasses have a more patchy distribution: *Pogonarthria squarrosa* (Roem. & Schult.), *Eragrostis obtusa* Munro ex Fical. & Hiern, *Enneapogon scoparius* Stapf, *Aristida meridionalis* Henr., *A. diffusa* Trin., *Themeda triandra* Forssk., *Digitaria eriantha* Steud. and *Chloris virgata* Swartz (Russell *et al.* 1991). The most common forbs are *Pentzia incana* (Thunb.) Kuntze, *P. spinescens* Less., *Gnidia polycephala* (C.A. Mey.) Gilg, *Geigeria filifolia* Mattf., *Dicoma capensis* Less., *Diospyros lycioides* Desf. and *Asparagus* species (Shearing 1994).

Experimental Design

The experiment entailed four treatments, each at two levels: (1) maximum-recorded rainfall *vs* natural rainfall; (2) nitrogen addition *vs* no addition; (3) burning *vs* no burning; and (4) grazing/clipping *vs* grazing exclusion. The same experimental design was used at each of the three sites, i.e. a completely-crossed randomized block with one replicate per treatment combination at each site. Assignment of treatments to experimental units was done independently for each site. Each treatment combination had three replicates (one at each site), to provide a total of 48 experimental plots (16 plots per site). Plots were 5 m by 5 m and spaced within 2 m to 10 m from each other. Plot size was chosen as the mean area where the asymptote of species-accumulation curves of all species in the field was reached. Plots were placed close to mature *A. mellifera* trees (to ensure seed availability) in areas of similar vegetation structure (i.e. open savanna with *c.* 25 % tree cover). No seeds (or seedlings) were added to the plots, but *A. mellifera* seeds collected at the study sites showed 100 % viability (tetrazolium chloride staining, Machlis & Torrey 1956) and 99 % germinability under laboratory conditions.

(1) Maximum-recorded rain vs Control (natural rainfall)

Control plots received natural rain only (230 mm from October 2000 to April 2001). In addition to the natural rain, irrigated plots were supplemented with the equivalent of the mean monthly rainfall. It was anticipated that the natural and applied rain would together amount approximately to the 120-year extreme of 978 mm. Maximum-recorded rain plots were irrigated twice monthly between October 2000 and April 2001. Each of the 14 applications added 32 mm over two hours; for the whole season a total of 448 mm was added (in addition to natural rainfall). Therefore, maximum-recorded rain plots received 678 mm during the whole season, which could still be considered as extremely high rainfall, because similarly high rainfall was only recorded three times since 1884 (see 'Study area', Fig. A). In terms of rainfall frequency, our watering regime consisted of fewer but larger rainfall events compared to natural rain.

(2) Nitrogen addition *vs* Control (no addition)

Plots supplemented with nitrogen received three equal applications, spread over the duration of the growing season, and evenly spread over the soil surface. A total of 168 kg N/ha was added in the form of limestone ammonium nitrate (600 kg LAN/ha). This was regarded as a high rate of nitrogen application in several studies (Le Roux & Mentis 1986; Tilman 1987a; Walker & Knoop 1987).

(3) Burning *vs* Control (no burning)

Burning of the grass was made difficult by the low herbaceous cover and biomass (even after an exceptionally good rainy season in 1999/2000). We used burning corncobs that were soaked in fuel to ignite individual grass tufts. In the opinion of the local people, fuel loads are generally insufficient due to low rainfall and grazing, rendering burning inapplicable in the area.

(4) Grazing/clipping *vs* Grazing exclusion

Plots to be protected from grazing were fenced off for the entire study period, excluding livestock and native ungulates. Heavy grazing was simulated by clipping the grass to ground level once a month. Clipped plots were not fenced and were thus open to additional grazing by livestock and native ungulates.

Monitoring

The number of emerging *Acacia mellifera* seedlings was counted and marked once every month. The survival of seedlings between emergence (first recorded December 2000) and the end of the growing season was also recorded. Soil samples were taken from the field plots prior to application of treatments as well as before the second nitrogen application (December 2000) and analysed for total nitrogen, using micro-Kjeldahl digestion followed by a standard indophenol-blue protocol (Alef & Nannipieri 1995).

Garden Experiment

The field experiment was replicated on a smaller scale, with some modifications, in a garden experiment. The garden experiment was set up in the open at the Conservation Ecology Department of the University of Stellenbosch, Stellenbosch (33°55' S, 18°52' E; 500 m a.s.l.), Western Cape, South Africa. The study was conducted during the summer months of November 2000 – April 2001. The dry summers of the Western Cape enabled artificial manipulation of the rainfall regime as well as providing a similar radiation regime to that of the field study site during the growing season.

Experimental Design

The experiment entailed three treatments, each at two levels: (1) high rain *vs* low rain; (2) nitrogen addition *vs* no nitrogen; and (3) clipping *vs* no clipping. The experiment had a completely-crossed design (eight different treatment combinations) with six replicates per treatment combination (a total of 48 experimental units). Treatments were randomly assigned to experimental units, which consisted of 80 *l* garbage bins (44 cm diameter *x* 62 cm height) filled with sterile sand (0.015 % N). A grass matrix of *Eragrostis curvula* (perennial) and *E. teff* (annual) was established during the first three months of the experiment, using seeds obtained from a local seed company. Thereafter, once the grasses were fully established, seeds of *A. mellifera* were sown (at a high density, i.e. 730 undamaged seeds per square meter) into the grass matrix at the beginning of February 2001. The tree seeds were collected at the field study site during December 2000/January 2001 and showed 100 % viability (tetrazolium chloride staining, Machlis & Torrey 1956). Laboratory germination was compared among three different pre-treatments, i.e. concentrated sulphuric acid (soaked for 20 min), boiling water and control (no treatment). Germination was high throughout, i.e. 70 %, 91 % and 99 % respectively (n=100). Based on these results, seeds were not pre-treated before sowing. At the onset of the experiment, high rain treatment bins received water to soil saturation every third day. When none of the *A. mellifera* seeds germinated, despite high seed viability and germinability, the watering frequency was increased to every second day (though less water per application) and the seed were covered with a thin layer of sand. These changes resulted in germination. Throughout the experiment dry bins were watered once in ten days. Nitrogen addition treatments received a total of 185 kg N/ha as 28 % LAN, and divided into four applications (this is regarded a high level of fertilization, e.g. Tilman 1987a). The controls received 18 kg N/ha at the onset of the experiment, just to enable grass growth in the sterile sand. The grass in the clipping treatments was clipped once every ten days.

Monitoring & Harvesting

Tree seedling germination was recorded regularly (every 7–10 days) throughout the period the experiment was running. Light intensity was measured at ground level with a quantum sensor (Licor Model LI-189, Lincoln, USA) towards the end of the experiment. Ten readings at random placements were taken per bin to obtain an indication of grass density and amount of light available to seedlings. Soil moisture was analysed by taking two soil cores (1 cm diameter *x* 10 cm height) per bin, one day after application of high rain treatments and ten days after application of low rain treatments. Soil was weighed before and after drying it for 48 hours at 60 °C. The experiment was terminated at the beginning of April 2001, two months after *A. mellifera* seed was sown, due to the start of the winter rains. The number of surviving tree seedlings was recorded before harvesting.

The shoots were cut at ground level, oven dried (48 hours at 60 °C) and weighed. Grass height was also measured before the grass shoots were harvested, dried and weighed.

Analysis

After testing for normal distributions with Kolmogorov-Smirnov (Lilliefors option), and for homogeneity of variance with Levene's test, all variables were Box-Cox transformed (Krebs 1989), because neither log- nor squareroot-transformations produced normally-distributed data. For the field experiment, effects of different treatments and treatment combinations on tree recruitment were analysed with randomized block ANOVAs, with site as a block. In addition, the tree germination data were subjected to non-parametric sign tests (Siegel & Castellan 1989), investigating the effects of rain and grazing only. Site B had the highest (and least variable) germination; we used a paired t-test to test for effects of rain and grazing at this site and did statistical power analysis (Cohen 1988; Samuels 1989) for the grazing treatment. In a single factor ANOVA, followed by Scheffe's *post hoc* test, we determined whether soil nitrogen content (prior to application of treatments) differed between sites. We also compared the percentage soil nitrogen of nitrogen addition treatments with controls by means of a t-test. Multi-factor ANOVAs were performed on the following parameters from the garden experiment data: seedling germination, survival and biomass, percentage soil moisture and light intensity at ground level. The relationship between light intensity and grass biomass was established by means of regression. Statistica (v. 5.5, 1984-2000, StatSoft Inc.) was used for Kolmogorov-Smirnov tests, Levene's tests, ANOVAs, regression and t-tests.

2.4   Results

Field Experiment

Climate

Comparing climatic conditions during the study season with long-term weather data revealed the following noteworthy differences: Natural rainfall received during the study season (October 2000 to April 2001) amounted to 230 ± 22 mm (mean of three sites $\pm$ 95 % confidence limits), which was 67 % of the long-term mean for these months, the latter being 341 ± 54 mm (mean $\pm$ 95 % confidence limits). The months of October and December 2000 and January and February 2001 were particularly dry compared to the long-term figures, while March 2001 had above average rains (Fig. 2.1). Humidity figures confirmed that January and February 2001 were dry months, being

50

significantly lower than the long-term means for these months. A trend towards longer sunshine hours (less cloud cover) for January and February 2001 and higher average wind speeds from January through March 2001 further aggravated the short-term 'drought'.
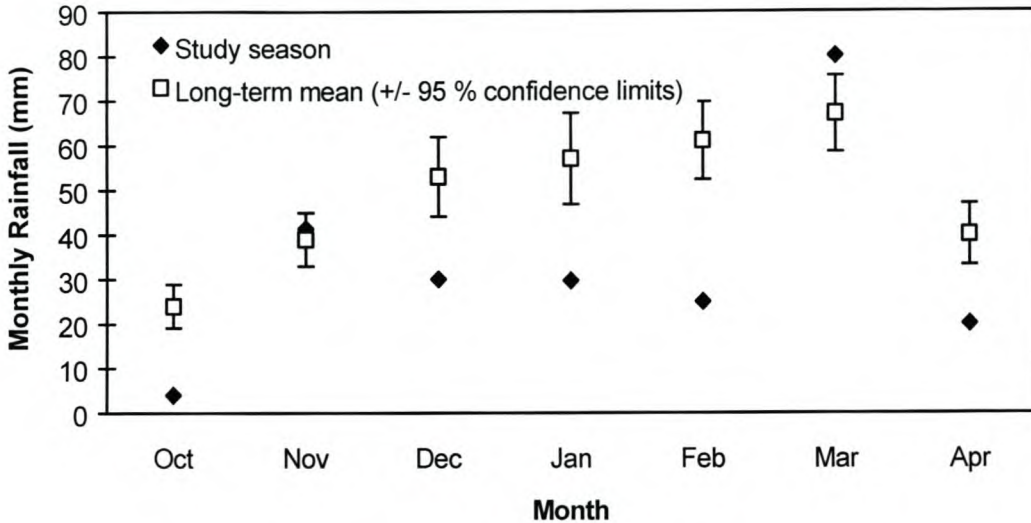
Figure 2.1: Comparison of natural rainfall during the study season (October 2000 – April 2001, Pniel) with long-term means (1884 – 2000, Barkly West).

Soil

The soil nitrogen content of site A (0.17 % $\pm$ 0.01, mean $\pm$ SE) was significantly higher than those of sites B (0.10 % $\pm$ 0.01) and C (0.09 % $\pm$ 0.01) ($F_{1,45}$=37.66, p<0.001). Three months after the first application of fertilizer, the mean soil nitrogen content of nitrogen addition plots (0.16 % $\pm$ 0.03, mean $\pm$ SE) was higher than those that did not receive fertilizer (0.12 % $\pm$ 0.02), though not significantly higher (t=1.49, p=0.082 (one-tailed test), df_{error}=10). The lack of significance may be ascribed to small sample size and large variance among sites A, B and C, which obscured the difference between nitrogen addition and control plots. However, the effect of nitrogen enrichment was clear from the lush growth and blue-green colour of the grasses in fertilized plots.

Recruitment

Despite good seed set in the field during the study season, *Acacia mellifera* germination was extremely low and highly variable. The mean number of seedlings that germinated per plot during the whole growing season was 7.1 $\pm$ 2.8 (mean $\pm$ SE), with a C.V. of 280 %. As a result of the low germination and high variability, there were no significant effects of any treatment (rain/nitrogen/fire/grazing) on tree recruitment by means of ANOVA. A comparison of germination

51

between treatments and controls for the three sites grouped together, using non-parametric sign-tests, also did not yield significant results. The direction of change in germination between treatments and controls showed trends opposite to our predictions for all treatments except nitrogen addition (Table 2.1). Among the three sites, site B had the highest germination with the least variation. When only site B was considered, rain significantly enhanced tree germination (t=2.88, p=0.006 (one-tailed test), df_{error}=14). Grazing did not have a significant effect on tree germination at site B (t=0.348, p=0.369 (one-tailed test), df_{error}=14). The actual effect size of the grazing treatment at site B was small (between 0.19 and 0.29), resulting in a power of 10–13 % to reject a false null hypothesis (at the 95 % confidence level). Thus, the lack of significant difference is likely to be due to Type II error.

Table 2.1: Percentage and direction of change in tree germination between controls and treatments. Results are shown for the field sites grouped, site B separately, and for the garden experiment. Signs (+/-) indicate the direction of change from controls, where + denotes higher germination in treatment than control and *vice versa*.

Treatment	Predicted direction of change from controls	Percentage and direction of change from controls		
		Field: all sites	Field: site B	Garden experiment
Rainfall	+	- 23	+ 1375	+ 2631
Nitrogen	-	- 76	- 78	- 36
Grazing	+	- 33	+ 57	+ 30
Fire	+	- 36	+ 63	N/A

Garden Experiment

Percentage soil moisture was significantly affected by all treatments, i.e. rain (F1, 40=1293.47, p<0.001), nitrogen (F1, 40=37.44, p<0.001) and clipping (F1, 40=8.79, p=0.005). High rainfall, no nitrogen addition and clipping (the latter two cases being due to reduced soil water extraction by grasses) resulted in moister soils. There was a significant negative relationship between grass shoot biomass and light intensity at ground level (r=0.78, F1,22=34.29, p<0.001). Light intensity was significantly lower under conditions of high rainfall (F1,40=16.79, p<0.001), nitrogen addition (F1,40=47.80, p<0.001) and no clipping (F1,40=722.32, p<0.001). There was also a significant interaction effect between nitrogen addition and clipping (F1,40=31.42, p<0.001) – clipping had a more pronounced effect on light intensity under conditions of nitrogen addition, and nitrogen addition had a larger effect when grasses where clipped. Similar to the results on light intensity, high rainfall (F1,20=20.25, p<0.001) and nitrogen addition (F1,20=159.23, p<0.001) increased grass shoot biomass in unclipped treatments. Grass height was also higher under high rainfall (F1,20=8.529, p<0.001) and nitrogen addition (F1,20=36.674, p<0.001) treatments. Light intensity,

grass height and grass shoot biomass show similar results as these are all related to grass density, the latter being a measure of the competition grasses pose to tree seedlings. The inverse of these results is reflected in percentage soil moisture (high grass densities accounting for higher water consumption).
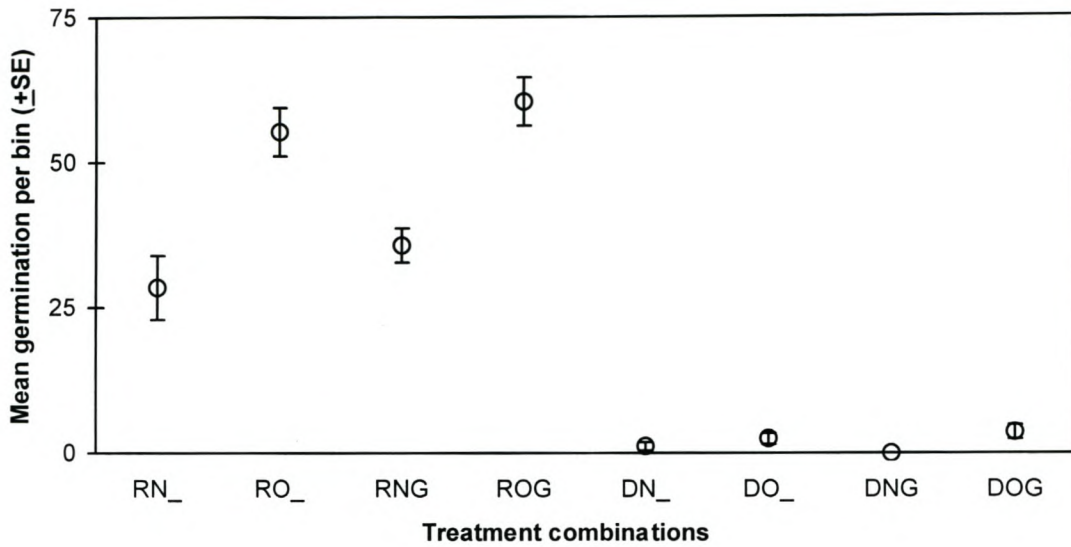
Germination

Germination results from the garden experiment matched our predictions remarkably well (Table 2.1). ANOVA results show that the rain ($F_{1,40}$=185.33, p<0.001) and nitrogen ($F_{1,40}$=64.19, p<0.001) treatments had significant effects on *A. mellifera* germination, germination being highest under conditions of frequent watering and no nitrogen addition (compare Table 2.1). There were also significant interaction effects between rain and nitrogen ($F_{1,40}$=46.26, p<0.001) and among rain, nitrogen and grazing ($F_{1,40}$=4.19, p=0.047). Rating the importance of each treatment in its effect on tree germination, it is clear from Fig. 2.2 and Table 2.1 (showing the percentage change between controls and treatments) that rain had an overriding influence, followed by nitrogen, while clipping (simulating grazing) was least important. Germination of *A. mellifera* seed was also critically dependent on rainfall frequency, and only occurred when the watering frequency was increased from every third day to every second day.

Survival

Most treatments and interactions significantly affected percentage seedling survival (after two months) i.e. rain ($F_{1,40}$=85.09, p<0.001), nitrogen ($F_{1,40}$=19.34, p<0.001), clipping ($F_{1,40}$=6.25, p=0.016), rain x nitrogen ($F_{1,40}$=19.30, p<0.001) and rain x clipping ($F_{1,40}$=6.23, p=0.016). Survival was enhanced by frequent watering, control nitrogen (no nitrogen addition) and grass-clipping.

Seedling Mass

The data on seedling mass at harvest showed much the same trend as germination and survival (Fig. 2.3). However, we excluded the dry treatments from the ANOVA on seedling mass, due to the fact that there were no surviving seedlings in all the replicates of two treatment combinations (i.e. low rain x nitrogen x no clipping and low rain x nitrogen x clipping). Nitrogen ($F_{1,20}$=237.44, p<0.001), clipping ($F_{1,20}$=53.81, p<0.001) and the interaction between the two ($F_{1,20}$=39.04, p<0.001) significantly affected the mass of seedlings in the high rain treatments. Seedlings were larger under rain, no nitrogen addition and clipping treatments.

Figure 2.2: Comparison of the number of *Acacia mellifera* individuals germinated among the different treatment combinations (garden experiment). Open dots indicate means of six replicates ± SE. R = Rain (high rainfall); D = Dry (low rainfall); N = Nitrogen addition; O = No nitrogen addition; G = Grazing/clipping; and _ = No clipping.
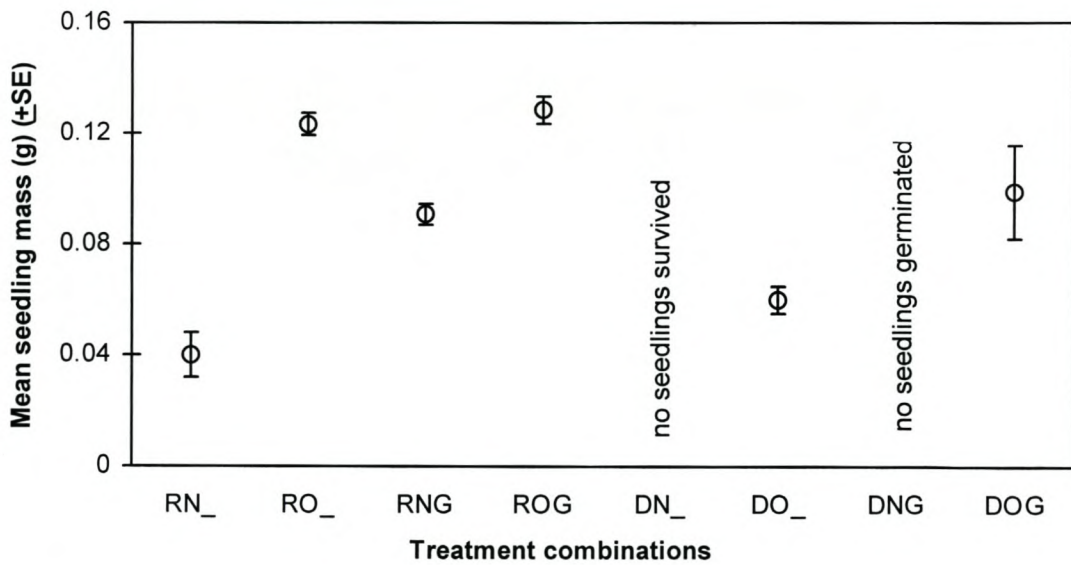
Figure 2.3: Comparison of *Acacia mellifera* seedling mass (at harvest) among the different treatment combinations (garden experiment). Open dots indicate means ± SE. R = Rain (high rainfall); D = Dry (low rainfall); N = Nitrogen addition; O = No nitrogen addition; G = Grazing/ clipping; and _ = No clipping.

2.5   Discussion

Tree germination in the field was extremely low, probably due to below-average rainfall in plots that only received natural rain, and insufficient watering frequency in irrigated plots. We inferred the latter from the garden experiment results showing that constant water availability (i.e. frequent rain) was the single most important factor initiating mass germination and survival (*cf.* Schultz *et al.* 1955; Wiegand *et al.* 1999). By means of a simulation model, Skarpe (1990b) demonstrated that daily soil moisture conditions (on which tree recruitment depends) are more sensitive to changes in timing and size of rains than to moderate differences in total seasonal rainfall or vegetation parameters. Wilson and Witkowski (1998) found that frequency of rainfall was crucial for *Acacia* germination and early survival (first seven weeks), more so than total amount of rain. Seeds required a critical level of soil moisture for about 10-14 days before emergence, while the minimum water requirements for the first two weeks of establishment were 3 mm of rainfall every second day. These conditions are probably only episodically met (during above-average rainfall periods), when cohorts of seedlings establish, with long periods of time when no or very few seedlings establish. Severe trampling (cattle were particularly attracted to the (unfenced) irrigated plots during the warm dry months) likely further reduced tree seedling establishment, as was found for perennial grass seedlings (Salihi & Norton 1987) and woody seedlings (Pitt *et al.* 1998; Kanz 2001).

Low germination in the field experiment and exclusion of fire from the garden experiment unfortunately prevented us from demonstrating the influence of burning on early tree establishment. Nevertheless, we expected that early spring (pre-germination) burns (if at all possible) would have minimal effects on early tree recruitment in semi-arid rangelands under grazing conditions, due to low herbaceous biomass. In other words, removal of the little grass present (after grazing) by fire should not drastically improve resource availability for tree seedlings. Accordingly, Higgins *et al.* (2000) predicted that in arid savannas, where fires are less intense and more infrequent, rainfall-driven variation in recruitment is more important to seedling establishment. Germination of the study species is also not dependent on seed banks from previous years (Smit GN *pers. comm.* 2000), and destruction of seed banks by early-season fires consequently need not be considered in this case. Although not part of this study's focus, one needs to keep in mind that fire may have a profound role in tree-grass dynamics by causing top-kill of established trees within the flame zone (Du Toit 1972a; Trollope 1974, 1980, 2000; Roberts 1986).

Acacia mellifera seedlings did not exhibit shade intolerance in either field or garden experiment. Seedlings germinated (and survived in the garden experiment) in the open areas between grass tufts, right next to tufts and even within tufts. From this we can infer that the negative influence of a dense grass sward on early *A. mellifera* establishment (as seen from lower tree germination and

seedling mass in unclipped bins than clipped bins, Fig. 2.2 & 2.3) should be ascribed to below-ground competition (for water and nutrients) rather than above-ground competition for light.
A. karroo seedlings have similarly been found to be tolerant to shade (O'Connor 1995), unlike *A. tortilis* (Kanz 2001) and some Australian *Acacia* species (Milton 1980). It can be expected that the trait of shade tolerance should improve a tree species' ability to invade/encroach a grass-/shrubland, enhancing the tree's competitive ability during its most vulnerable life stage (i.e. as seedling). However, compared to a shade-tolerant species, a shade-intolerant species should benefit relatively more from pre-germination fires or grazing, both through a reduction in above- and below-ground competition, whereas a shade-tolerant species will only gain from the reduction in below-ground competition. It is possible that a species' germination and initial establishment phases are shade-tolerant, while intolerance to shade during later life stages may be a consequence of trade-offs with other fitness traits.

According to Wilson (1988), below-ground competition between tree seedlings and grasses is of overriding importance when resources (water and nutrients) are poor, while above-ground competition (primarily for light) becomes significant when water and nutrients are plentiful. In a semi-arid savanna this is likely to be true, as light is not limiting, but resources are poor. On this basis, one would expect when resources are abundant (i.e. under high rain and nitrogen addition treatments in this study's garden experiment) that the alleviation of above-ground competition (through clipping) should be of relatively greater advantage to tree seedlings than when a resource, e.g. nitrogen, is limiting (compare the difference in tree seedling germination and biomass between RNG (high rain x nitrogen addition x clipping) and RN_ (high rain x nitrogen addition x no clipping) with the difference between ROG (high rain x no nitrogen x clipping) and RO_ (high rain x no nitrogen x no clipping), Fig. 2.2 & 2.3). Our garden experiment results on tree seedling biomass (Fig. 2.3) supported Wilson's (1988) predictions: without nitrogen limitation, clipping the grasses increased tree seedling mass to a greater extent than under nitrogen-poor conditions. The tree germination results did not exhibit as clear a trend (Fig. 2.2), although there was a significant interaction effect between rain, nitrogen and grazing. Nitrogen supplementation stimulated grass growth, which in turn likely reduced a resource required by *Acacia mellifera* seedlings and this limitation reduced tree seedling growth. In a similar experiment, Van Auken *et al.* (1985) showed that *Acacia smallii* (growing with *Celtis laevigata*) did not respond to nitrogen addition, and hence a second resource (e.g. phosphorus, potassium, magnesium, iron or water) may have been limiting (Cohn *et al.* 1989). To summarize, we demonstrated that changes in soil nitrogen could alter the competitive outcome between *A. mellifera* and *Eragrostis* grass species due to different soil nitrogen requirements of these species. This is congruent with other studies showing that modifications of nutrient levels caused changes in competitive relationships, affecting both the

intensity and outcome of competition (Bazzaz & Harper 1976; Fowler 1982; Cohn *et al.* 1989). Similarly, Van Auken *et al.* (1985) ascribed the ability of *A. smallii* to colonize areas where intense grazing and/or farming have depleted the soil of available nitrogen to its tolerance of low levels of soil nitrogen.

Our garden experiment results, which showed that grazing (clipping) was least important among the treatments, in addition to the fact that heavy grazing on its own could not elicit significant tree seedling establishment in the field, lead us to infer that grazing was not the overriding influence on tree recruitment. The field experiment showed that the direction of change in tree germination due to grazing (compared to controls) was opposite to what we predicted (Table 2.1). There was thus no need for statistical power analysis, as Type II error could not have caused this result. However, at site B, change was in the predicted direction (i.e. higher recruitment with grazing, Table 2.1), but low sample size and large variability resulted in low power to reject a false null hypothesis. To conclusively reject a false null hypothesis, given our small effect size (the change as result of a treatment), the sample size would have had to be very large (i.e. >>124, Samuels 1989). For this reason, we could not categorically say that grazing did not affect tree germination. We stress, however, that the power needed to reject a false null hypothesis should, strictly speaking, be calculated on the basis of an effect size determined *a priori* (Cohen 1988), based on the minimum acceptable difference in means of treatment and control, or from data obtained from a pilot study. However, in field ecology we frequently do not have an *a priori* expectation of effect size (Peterman 1990). Thus, the power reported here should be treated with some circumspection. In terms of management, power analysis with *a priori* determination of effect size is an important tool in decision-making and planning, because *a priori* effect sizes can be determined on economic grounds. For instance, a field manager might want to detect a given effect size as result of a particular management action (e.g. grazing), because he knows that above that level of change (let's say a 50 % increase in tree abundance), cattle ranching is no longer economically viable. He can then calculate the sample size necessary to detect that 50 % change with reasonable power (e.g. 80 % power at the 95 % confidence level). Based on these criteria, the sample size (number of plots) should be at least 64 in this investigation (Samuels 1989).

Our results on the significance of grazing for tree recruitment are in accordance with the findings of Brown and Archer (1989) and contrary to the widespread assumption that heavy grazing is required for tree encroachment in savannas. Bush and Van Auken (1995) argued that grass defoliation will have a significant (positive) effect on tree seedling performance when compared to the negative effect of high grass biomass on tree seedlings (they showed that tree seedlings suffered 100 % mortality due to grass competition where the grass density was *c.* 800 g/m^2). As a consequence,

57

these authors attributed Brown and Archer's (1989) results (i.e. clipping not affecting tree recruitment) to insufficient grass biomass (500 – 600 g/m^2) to suppress tree recruitment. This lower grass biomass was comparable to that in our garden experiment - ranging from 214 g/m^2 in dry, not-fertilized, unclipped treatments to 686 g/m^2 in watered, fertilized, unclipped treatments. Contingent upon this argument that grasses outcompete trees for resources at sufficiently high densities/biomass, one would expect that the tree seedlings in our low rain ($\approx$low grass biomass) treatment would fare better than in the high rain ($\approx$high grass biomass) treatment. However, the opposite was true. We furthermore doubt that grass densities as high as in Bush and Van Auken's (1995) study are realistically attainable and the norm in semi-arid and arid rangelands, considering that the highest grass density we measured in the open at our field study site (at a 1 m^2 scale) was 370 g/m^2. It is therefore unlikely that cessation/reduction of grazing pressure will in itself prevent bush encroachment under prevailing conditions in dry savannas.

To summarize, given that rainfall conditions are adequate, nitrogen addition retards bush encroachment while grazing increases it, grazing being the least important of these three factors. Our results showing that significant tree recruitment occurs under above-average rainfall conditions only, imply that managers in semi-arid areas should be especially attentive to maintaining low stocking rates in wet years. This is contrary to traditional thinking, which advocates that care should mainly be taken not to overstock in dry years. At a landscape scale, we further predict that nitrogen-poor environments are more prone to bush encroachment. This prediction is supported by the widespread occurrence of bush encroachment on the nitrogen-poor Kalahari sands (Scholes 1990) of southern Africa (Joubert 1966; Donaldson 1966, 1967a; Skarpe 1990a,b; Hoffman *et al.* 1999), where veld degradation/high grazing pressure is also common (Hoffman *et al.* 1999).

A limitation of this study was the experimental period, which neglected dry season and post first season seedling survival. Consequently, the interpretation of results was limited to seedling establishment over a seedling's first growing season. Trends regarding the effects of causal factors on early tree establishment may not be reflected in adult populations (e.g. Kanz 2001). Management guidelines based on the results of this study are therefore relevant to the prevention of the initiation of bush encroachment. Whether these guidelines are also applicable to controlling later stages of woody encroachment needs be investigated. However, if woody seedlings are not controlled during the first growing season they may grow to a taller stage and escape the detrimental effects of future fires and/or their roots may grow below the maximum penetration level of grass roots so that moisture will be available to them in subsequent years (Schultz *et al.* 1955).

Results of our experiments were further dependent on the particular levels of all treatments applied, especially our ranking the importance of treatments relative to each other. We hoped to be able to evaluate if garden experiments are true representations of field conditions by comparing the field and garden experiment directly. Unfortunately we were not able to do this, firstly due to the very low germination in the field, and secondly due to the need to alter the watering regime of the garden experiment, because the watering frequency in the field was insufficient to trigger germination. As a result, the garden experiment represented a simplification of a natural community: plants were grown under conditions in which the density and proportion of species were controlled and most of the natural heterogeneity of the environment removed. Although the reduction in complexity provides an opportunity to isolate and measure the interactions among species and treatments, the cost to this simplification is that the extrapolation of conclusions from garden to natural community must be tentative. Lastly, we would like to mention that our investigation of the effects of nutrient enrichment was aimed at the mechanistic understanding of competition between grasses and tree seedlings, rather than trying to find a possible control measure for bush encroachment. However, this investigation did provide some predictive power in this regard *viz.* to identify (nutrient-poor) areas especially prone to encroachment by *A. mellifera*.

3.   EFFECTS OF RAIN, NITROGEN, FIRE AND GRAZING ON GRASS DYNAMICS

3.1   Abstract

The increase of woody vegetation in semi-arid ecosystems is largely attributed to reduced grass competition due to heavy grazing by mammalian herbivores. In a field experiment we investigated the effects of maximum-recorded rainfall, nitrogen addition, early-spring fire, heavy grazing and all possible interactions on grass species composition, grass cover, height and shoot biomass in the short term. All these parameters are related to the level of resistance the grass sward poses to tree establishment. Historical effects (site differences) were of overriding importance for community composition, relative to the effects of the treatments after one growing season. Grazing/clipping significantly reduced grass species richness. Grass cover and height (and consequently grass biomass) were significantly increased by high rainfall and significantly reduced by grazing. Nitrogen addition and fire did not significantly affect any of the grass parameters. The lack of significant effects of most treatments may be ascribed to the short study period in addition to the variation among sites.

Keywords: Tree-grass competition, grass composition, grass biomass, interaction effects.

3.2   Introduction

Increases in woody plant density with concomitant changes in herbaceous cover and composition (termed 'bush encroachment') have been documented in savannas worldwide (Kreuter *et al.* 1999, Johnson *et al.* 1993). The increase of woody vegetation in semi-arid ecosystems is largely attributed to reduced grass competition because of over-utilization by mammalian herbivores (Skarpe 1990a; Chirara *et al.* 1999). Herbivory influences plant competitive interactions in two ways: by changing plant access to resources through modifying plant growth or morphology; and by altering the resources available for competitors (Louda *et al.* 1990). During establishment, woody seedlings are likely to face competition from the grass layer (Bush & Van Auken 1990; Cohn *et al.* 1989). Sustained heavy grazing can reduce the grasses' above- and below-ground biomass, and resource use (Ellison 1960; Knoop & Walker 1985; Van Auken & Bush 1989; Holland & Detling 1990; Chirara *et al.* 1999), which may promote the establishment of tree seedlings due to increased irradiance at ground level and increased availability of below-ground resources (Caldwell *et al.* 1987). The positive effects of a reduction in grass competition (Bush & Van Auken 1995) on tree seedling recruitment may be modified by increased livestock pressure,

due to trampling (Pitt *et al.* 1998) and browsing pressure on woody seedlings (Belsky 1984), either by direct selection by browsers (e.g. goats), or by incidental grazing by cattle.

Many studies show that in an area of reduced grass competition an emerging woody seedling has a greater chance of establishing than a seedling emerging in a vigorous sward (e.g. Schultz *et al.* 1955; Knoop & Walker 1985; Bush & Van Auken 1990), although other studies challenge such findings (O'Connor 1995; Brown & Archer 1999). Even though grazing is the most frequently cited cause of bush encroachment (Joubert 1966; Madany & West 1983; Van Vegten 1983; McPherson & Wright 1990; Skarpe 1990a,b; Perkins & Thomas 1993; Schultka & Cornelius 1997), a reduction in competition by herbs via livestock grazing does not always improve woody seedling success, and studies generally produced mixed results (*cf.* Andersson 1856; Du Toit 1972a; Strang 1974; Brown & Archer 1989, 1999; Scholes & Walker 1993). Similarly, fire may have divergent effects on tree-grass competition, depending on its frequency, intensity and seasonality (*cf.* Joubert 1966; Du Toit 1972a; Trollope 1980, 1987; Medina & Silva 1990). An increase in nutrient availability has also been shown to improve the competitive ability of grasses over less nutrient-restricted (N_2-fixing) *Acacia* seedlings (Cohn *et al.* 1989). It is clear that no single factor controls the tree-grass ratio, it being further complicated by the vast number of potential interactions between these factors (Van der Schijff 1964; Donaldson 1967a). Despite not having a general and unequivocal explanation for the way trees and grasses interact, we do know that competition is a major process in community structure (Connell 1983; Schoener 1983; Goldberg & Barton 1992) and more specifically, bush-grass dynamics (Walter 1971; Walker *et al.* 1981; Stuart-Hill & Tainton 1988; Davis *et al.* 1998). Therefore, any factor that will affect the competitive ability of the herbaceous layer should ultimately influence woody encroachment.

The structure of the herbaceous vegetation should be related to the resistance tree seedlings would experience during establishment. In describing the features (including the structure) of herbaceous vegetation, grasses have conventionally been grouped according to their:

     (1) growth form (*tufted* or *creeping*);

     (2) longevity; and

     (3) reaction to different levels of grazing, or so-called 'ecological/grazing status' (Van Oudtshoorn 1999).

On the basis of their longevity, grasses can be classified as *annuals* (growing for only one season), *perennials* (living for more than one year), and *weak/facultative perennials* (living for only two to five years). Grasses are further grouped into *decreasers* (palatable climax grasses that decrease in over-/undergrazed veld); *increaser I* (unpalatable climax grasses that increase in underutilized veld); *increaser II* (pioneer and subclimax grasses abundant in heavily grazed veld); and

61

increaser III species (unpalatable, dense climax grasses common to heavily grazed veld) (Van Oudtshoorn 1999). The ecological-status criterion is often used to assess range condition (Smit & Rethman 1992; Van Oudtshoorn 1999). As the above classifications reflect herbaceous structure and 'condition', these may be useful in predicting the reaction of the community to perturbations and its susceptibility to tree encroachment. However, Belsky (1992) concluded that grass species (of the Serengeti) could not be divided into functional groups/guilds (e.g. based on grazing status) in which all species responded similarly to the major environmental factors. Instead, species height and life-history proved to be more useful for predicting the responses of grass species to environmental factors (Belsky 1992; O'Connor 1994) and possibly tree-grass interactions.

The major factors affecting savanna structure and functioning are rainfall, nutrients, fire and herbivory (Schultz *et al.* 1955; Frost *et al.* 1985; Knoop & Walker 1985; Van Auken *et al.* 1985; Walker 1987; Stuart-Hill & Tainton 1988, 1989; Teague & Smit 1992; Jeltsch *et al.* 1996; Higgins *et al.* 2000). This paper focuses on the influences of these factors on the herbaceous layer, and interaction effects among these factors. The specific objective was to determine the effects of rain, nitrogen, fire, grazing and all possible interactions on grass species composition, grass cover and height in the short term, all of these being related to the field condition as well as the level of resistance the grass sward poses to tree establishment.

3.3   Materials & Methods

Study Site

The study was conducted at three different sites on Pniel Estates near Barkly West (35 km north west of the city of Kimberley), Northern Cape, South Africa. The three sites were referred to as site A (28°36'11" S, 24°29'00" E; 1130 m a.s.l.), site B (28°36'11" S, 24°24'16" E; 1160 m a.s.l.) and site C (28°35'31" S, 24°22'45" E; 1150 m a.s.l.). The land used to be heavily grazed by various livestock, but since 1960, it has been moderately grazed by cattle in a multi-camp (rotational) system. The study period covered one growing season (October 2000 – April 2001). The mean annual rainfall (based on 84 records, kept since 1884) for Barkly West is 388 mm and it is extremely variable (C.V. = 39 %). Mean monthly minimum/maximum temperatures for Kimberley range between 3.2/18.2 °C in June and 17.9/32.8 °C in February with an average of 22 days of frost per year. The underlying rock at site A is andesite, while nutrient-poor red dune sand of aeolian origin predominates at sites B and C (Bosch 1993; Bezuidenhout 1994, 1995).

The vegetation type is semi-arid savanna, known as Kimberley Thorn Bushveld (Low & Rebelo 1998) or Kalahari Thornveld (veld type 16, Acocks 1988). There are scattered trees, mostly *Acacia erioloba* E. Mey. and *A. tortilis* (Forsk.) Hayne subsp. *heteracantha* (Burch.) Brenan while the shrub/low tree layer is dominated by *A. mellifera* (the main encroaching tree), *Grewia flava* DC. and *Tarchonanthus camphoratus* L. [*T. minor* Less.] (Palgrave 1977; Smit 1999). The herbaceous sward mainly consists of tufted perennial grasses, the most common species being *Eragrostis lehmanniana* Nees, *Schmidtia pappophoroides* Steud., *Stipagrostis uniplumis* (Licht.) De Winter and *Aristida canescens* Henr. (in order of decreasing abundance). The following grasses have a more patchy distribution: *Pogonarthria squarrosa* (Roem. & Schult.), *Eragrostis obtusa* Munro ex Fical. & Hiern, *Enneapogon scoparius* Stapf, *Aristida meridionalis* Henr., *A. diffusa* Trin., *Themeda triandra* Forssk., *Digitaria eriantha* Steud. and *Chloris virgata* Swartz (Russell *et al.* 1991). The most common forbs are *Pentzia incana* (Thunb.) Kuntze, *P. spinescens* Less., *Gnidia polycephala* (C.A. Mey.) Gilg, *Geigeria filifolia* Mattf., *Dicoma capensis* Less., *Diospyros lycioides* Desf. and *Asparagus* species (Shearing 1994).

Experimental Design

The experiment entailed four treatments, each at two levels: (1) maximum-recorded rainfall *vs* natural rainfall; (2) nitrogen addition *vs* no addition; (3) burning *vs* no burning; and (4) grazing/clipping *vs* grazing exclusion. The same experimental design was used at each of the three sites i.e. a completely-crossed randomized block with one replicate per treatment combination at each site. Assignment of treatments to experimental units was done independently for each site. Each treatment combination had three replicates (one at each site), to provide a total of 48 experimental plots (16 plots per site). Plots were 5 m by 5 m and spaced within 2 m to 10 m from each other. Plot size was chosen as the mean area where the asymptote of species-accumulation curves of all species in the field was reached. Plots were in areas of similar vegetation structure, i.e. open savanna with *c.* 25 % tree cover.

(1) Maximum-recorded rain *vs* Control (natural rainfall)

Control plots received natural rain only (230 mm from October 2000 to April 2001). In addition to the natural rain, irrigated plots were supplemented with the equivalent of the mean monthly rainfall. It was anticipated that the natural and applied rain would together amount approximately to the 120-year extreme of 978 mm. Maximum-recorded rain plots were irrigated twice monthly between October 2000 and April 2001. Each of the 14 applications added 32 mm over two hours; for the whole season a total of 448 mm was added (in addition to natural rain). Compared to natural rain, our watering regime consisted of fewer but larger rainfall events.

(2) Nitrogen addition *vs* Control (no addition)

Plots supplemented with nitrogen received three equal applications, spread over the duration of the growing season, and evenly spread over the soil surface. A total of 168 kg N/ha was added in the form of limestone ammonium nitrate (600 kg LAN/ha). This was regarded as a high rate of nitrogen application in several studies (Le Roux & Mentis 1986; Tilman 1987a; Walker & Knoop 1987).

(3) Burning *vs* Control (no burning)

Burning of the grass was made difficult by the low herbaceous cover and biomass (even after an exceptionally good rainy season in 1999/2000). We used burning corncobs that were soaked in fuel to ignite individual grass tufts. In the opinion of the local people, fuel loads are generally insufficient due to low rainfall and grazing, rendering burning inapplicable in the area.

(4) Grazing/clipping *vs* Grazing exclusion

Plots to be protected from grazing were fenced off for the entire study period, excluding livestock and native ungulates. Unfenced plots were open to grazing by cattle and native ungulates in addition to the grass being clipped to ground level once a month (October 2000 to February 2001). The last clipping was done in February to allow grasses to flower for identification purposes at the end of the experiment.

Monitoring

Soil samples were taken from the field plots prior to application of treatments as well as before the second nitrogen application (December 2000) and analysed for total nitrogen, using micro-Kjeldahl digestion followed by a standard indophenol-blue protocol (Alef & Nannipieri 1995). To determine initial variability in herbaceous vegetation between plots and sites, grass and forb height and cover were measured with a point-frequency frame (Levy & Madden 1933; Mueller-Dombois & Ellenberg 1974; Cook & Stubbendieck 1986) prior to application of treatments (September 2000). Thereafter, grass and forb cover and height were monitored in the same way once every month. At the end of the growing season grass biomass was estimated on the basis of a regression between grass biomass and grass height. To establish the relationship between grass biomass and grass height, we harvested, dried (48 hours at 60 °C) and weighed above-ground grass biomass from 55 random samples of 1 m^2 each (25 units at site A and 30 at site B), and took point-frequency frame readings of grass height from the same samples.

Analysis

In a single factor ANOVA, followed by Scheffe's *post hoc* test, we determined whether soil nitrogen content (prior to application of treatments) differed between sites. We also compared the percentage soil nitrogen of nitrogen addition treatments with controls by means of a t-test. The relationship between grass biomass and grass height was established by means of regression for site A and B and the residuals compared by a t-test. Shannon-Weaver index of diversity and Simpson's index of dominance and richness were calculated for the herbaceous layer, using a multivariate statistical package (MVSP v. 3.12d, 1985-2001, Kovach Computing Services). Using the same statistical package, we performed detrended correspondence (indirect gradient) analyses (DCA) and canonical correspondence (direct gradient) analyses (CCA) to compare plots in terms of possible effects of site and treatments on grass species presence/absence (i.e. abundance) and on grass cover and height. After testing for normal distributions with Kolmogorov-Smirnov (Lilliefors option) and for homogeneity of variance with Levene's test (using Statistica), all variables except grass species diversity were Box-Cox transformed (Krebs 1989), because neither log- nor squareroot-transformations produced normally-distributed data. The effects of the different treatments and treatment combinations on forb cover and grass composition, cover, height and biomass were then analysed in randomized block ANOVAs, with site as block. Statistica (v. 5.5, 1984-2000, StatSoft Inc.) was used for Kolmogorov-Smirnov tests, Levene's tests, ANOVAs, regression and t-tests.

3.4   Results

Site A (0.17 % ± 0.01, mean ± SE) had a significantly higher soil nitrogen content than sites B (0.10 % ± 0.01) and C (0.09 ± 0.01) ($F_{2,45}$=30.86, p<0.001), sites B and C being similar. Three months after the first application of fertilizer, the mean soil nitrogen content of nitrogen addition plots (0.16 % ± 0.03, mean ± SE) was higher than those that did not receive fertilizer (0.12 % ± 0.02), though not significantly higher (t=1.49, p=0.082 (one-tailed test), df_{error}=10). The lack of significance may be ascribed to small sample size and large variance among sites A, B and C, which obscured the difference between nitrogen addition and control plots. However, the effect of nitrogen enrichment was clear from the lush growth and blue-green colour of the grasses in fertilized plots.

There was a significant positive relationship between grass height and biomass at both site A
(r=0.96, $F_{1,23}$=281.79, p<0.001) and site B (r=0.90, $F_{1,28}$=124.53, p<0.001) (Fig. 3.1). The biomass-
height relationships differed significantly between the two sites (t=2.25, p=0.014, df_{error}=53). It was
clear from the CCA (performed on grass species abundance and grass cover and height data) that
plots could not be separated on the basis of treatments or combinations thereof. Site proved to be
the only significant factor in producing the observed separation of plots, site A being opposite to
site B (Fig. 3.2, graphical results are only presented for grass species abundance, as this was
representative of the other parameters considered). The overall grass cover (mean of the three
study sites) was 48.7 % and cover of forb species 5.3 % (Table 3.1). *Eragrostis lehmanniana* was
the most abundant grass with an overall cover of 17.3 %, followed by *Schmidtia pappophoroides* at
12.5 % (Table 3.1). The herbaceous layer at site A was dominated by *Aristida canescens* and
E. lehmanniana, at site B by *Schmidtia pappophoroides* and *Stipagrostis uniplimis*, and at site C by
E. lehmanniana and *Schmidtia pappophoriodes*. *A. canescens* occurred almost exclusively at
site A and *Stipagrostis uniplumis* mostly at site B.

None of the treatments, interactions or site had a significant effect on grass species diversity or
dominance in the randomized block ANOVA. We found significant effects of both site and grazing
on grass species richness ($F_{2,29}$=6.09, p=0.006 and $F_{1,29}$=7.93, p=0.008 respectively).
Grazed/clipped plots had fewer grass species (2.61 ± 0.20, mean ± SE, n=24) than plots from
which grazing was excluded (3.26 ± 0.21, mean ± SE, n=24). Percentage forb cover was only
affected by site ($F_{2,30}$=6.02, p=0.006; see also Table 3.1) and the interaction between all four
treatments ($F_{1,30}$=4.23, p=0.048). Percentage grass cover was also significantly affected by site
($F_{2,29}$=5.49, p=0.009), as well as rain ($F_{1,29}$=51.95, p<0.001), grazing ($F_{1,29}$=256.56, p<0.001) and
the interaction of fire, nitrogen and grazing ($F_{1,29}$=7.57, p=0.010). Similarly, grass height was
significantly affected by site ($F_{2,29}$=4.45, p=0.020), grazing ($F_{1,29}$=573.49, p<0.001) and the
interaction between rain and grazing ($F_{1,29}$=13.84, p<0.001). Grass cover and height combined
give an indication of grass biomass. Thus, rain ($F_{1,30}$=16.23, p<0.001) and grazing ($F_{1,30}$=413.87,
p<0.001) (but no interactions) significantly affected grass biomass. Site was the only factor that
had significant effects on the proportion of tufted perennial grass species as opposed to weak
(facultative) perennials ($F_{2,30}$=10.78, p<0.001), and also the proportion of Increaser II *vs* Increaser
III species ($F_{2,30}$=42.57, p<0.001) (as classified by Van Oudtshoorn 1999).

Table 3.1: Mean percentage cover of the respective grass species (in order of decreasing overall abundance), forb species (grouped) and bare soil at the different study sites (A, B & C) and calculated for the three sites together (termed overall). The survey was done with a point-frequency frame, with the percentage cover being equivalent to probability of occurrence. Note that these data are not the data used in the ANOVA above (performed on all grass species collectively).

Species	Site A % cover	Site B % cover	Site C % cover	Overall % cover
Eragrostis lehmanniana	14.4	8.0	29.5	17.3
Schmidtia pappophoroides	0.1	21.4	16.0	12.5
Stipagrostis uniplumis	0.6	20.9	1.8	7.8
Aristida canescens	20.9	0.6	0.3	7.3
Pogonarthria squarrosa	0	4.4	2.3	2.2
Eragrostis obtusa	3.8	0	0	1.3
Enneapogon scoparius	1.1	0	0	0.4
Aristida meridionalis	0	0.4	0	0.1
Forb species	4.9	1.8	9.3	5.3
Bare soil	54.3	42.6	41.0	46.0
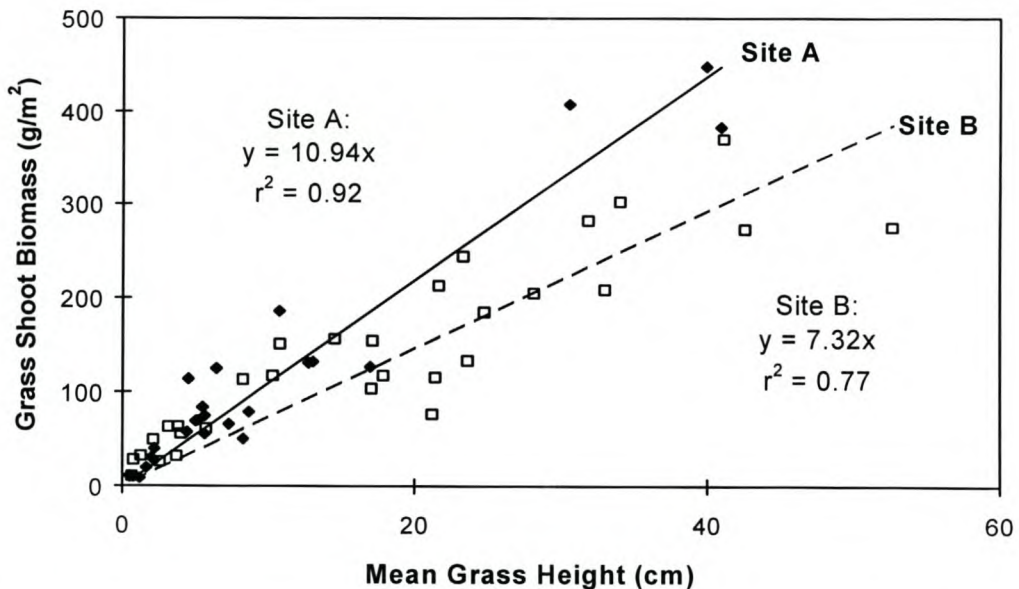
Figure 3.1: Relationship between above-ground grass biomass and mean grass height per sampling unit (as measured by a point-frequency frame) for site A (♦) and site B (□) respectively. For each site the best-fit linear regression, regression equation and r^2-value are shown.

67
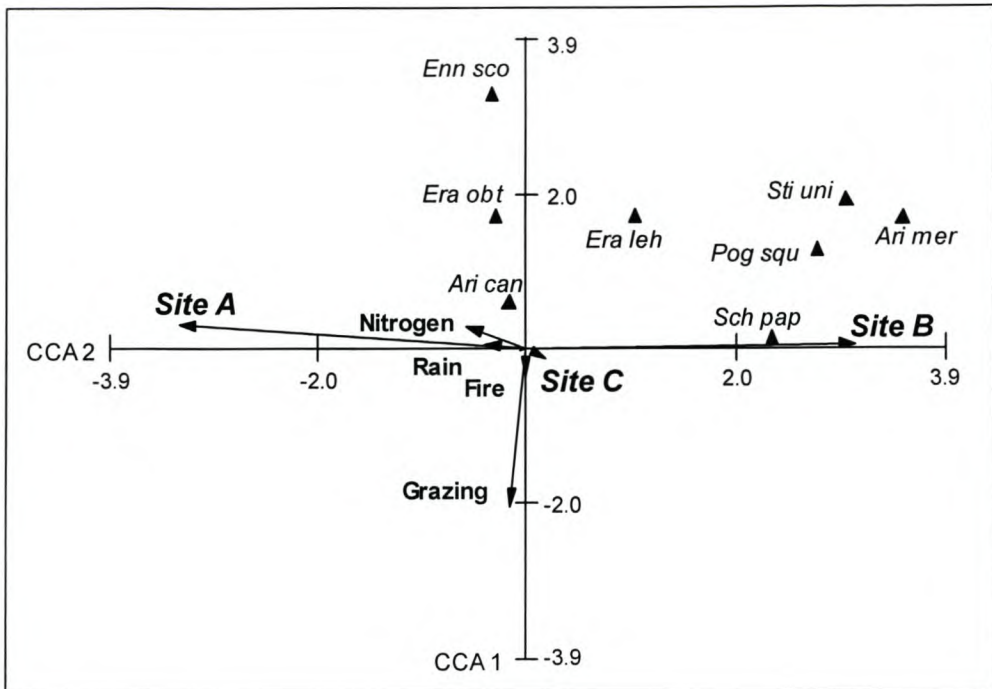
Figure 3.2: Plot of 1st and 2nd canonical correspondence axes from a detrended canonical correspondence analysis (CANOCO) ordination of grass species abundances, comparing plots in terms of possible effects of site (sites A, B & C) and treatments (rain, fire, nitrogen and grazing). Plots could only be separated on the basis of site differences, probably as a result of initial site differences and differences in soil type. Grass species (▲) are abbreviated as follows: *Ari can = Aristida canescens; Ari mer = A. meridionalis; Enn sco = Enneapogon scoparius; Era leh = Eragrostis lehmanniana; Era obt = E. obtusa; Pog squ = Pogonarthria squarrosa; Sch pap = Schmidtia pappophoroides;* and *Sti uni = Stipagrostis uniplumis.*

3.5   Discussion

Community composition

The significance of site in influencing most grass parameters (richness, grass type/status, cover, height and biomass) and forb abundance was clear from both the ordination analyses and analyses of variance. From this we infer that historical effects (initial site differences) were of overriding importance relative to the treatments after only one growing season. However, the short period over which the treatments were applied (October 2000 - April 2001) likely explains why vegetation composition was not significantly affected by the treatments. O'Connor and Pickett (1992) also found that compositional variation in grasslands reflected the grazing history of sites (see also Lenzi-Grillini *et al.* 1996). Differences in species composition may further be accounted for by soils

68

differing among sites, soils being more clayey and with higher total soil nitrogen at site A than at sites B and C. The significant difference between the grass biomass-height relationships of site A and site B, and the significant effects of site on grass type (type of perennial and grazing status), confirm the difference in community composition between the sites.

Rainfall

Various studies, both long- and short-term, have emphasized the overriding influence of rainfall on grass composition, abundance, recruitment, mortality and production, in that it makes the influence of other factors, such as shading, litter, grazing etc. appear relatively insignificant (e.g. Tinley 1982; O'Connor 1985, 1993, 1994; Stuart-Hill *et al.* 1987; Scholes 1990). This should be especially true for water-restricted systems, such as semi-arid savannas. However, we only found grass cover and biomass to be significantly affected by rainfall, while grazing had a larger effect on both parameters than rainfall. High rainfall also significantly increased above-ground grass biomass in a garden experiment (Chapter 2), although rainfall had a smaller effect than nitrogen addition and grazing. We can conclude that rainfall was not the overriding influence on the grass parameters we measured, although the importance of rainfall was augmented by its interactions with other factors (see 'Interaction effects').

Grazing

Our results of heavy grazing significantly suppressing grass cover, height and biomass were to be expected and are in accordance with the findings of other studies (e.g. Ellison 1960; Du Toit 1972b; Van Auken & Bush 1989; Lenzi-Grillini *et al.* 1996). It would have been ideal to exclude grazing from the grazed/clipped treatments for a season after the study period, to determine if one season's heavy grazing had any long-term detrimental effects on grass productivity (due to below-ground resource depletion, Van Auken &Bush 1989; Bush & Van Auken 1995; Rice *et al.* 1998). However, because these plots were not fenced, they remained open to grazing by cattle and native ungulates after clipping had ceased, which rendered such an investigation inappropriate. Heavy grazing has repeatedly been shown to alter species composition (e.g. Janse van Rensburg 1939; Ellison 1960; Du Toit 1972b; Belsky 1992; Smit & Rethman 1992; O'Connor & Pickett 1992; O'Connor 1994). Accordingly, we found heavy grazing/clipping to significantly reduce grass species richness. Grazing did not significantly affect the relative abundance of grasses grouped according to grazing status. This may be explained by the sward only consisting of increaser II and increaser III species, which both, by definition, should increase as a result of heavy grazing. Thus, we cannot comment on the value/suitability of this classification system for predicting the response of grasses to environmental factors.

Nitrogen

Fertilization has been widely shown to affect community-, and in particular, grass species diversity, usually causing a loss of diversity (Roux & Warren 1963; Mills 1964; Grunow *et al.* 1970; Le Roux & Mentis 1986; Tainton 1984; Tilman 1987a; Van Andel & Van den Bergh 1987; Seastedt *et al.* 1991). Rosenzweig (1971) termed this reduction in diversity due to nutrient enrichment the 'paradox of enrichment', which corresponds to the intermediate-productivity hypothesis. The latter states that diversity peaks at intermediate levels of productivity (Grime 1979), while diversity is restricted by competition at both extremes of productivity (high and low). However, exceptions to this trend occur, e.g. Walker and Knoop (1987) showed that species composition was unaffected by four years of fertilizer application. Similarly, nitrogen addition in our experiment did not significantly alter species diversity/dominance/richness, although the lack of a significant result may be ascribed to the short study-period. Grass cover was not significantly affected by nitrogen addition in our study, similar to the results of Grunow *et al.* (1970) after three seasons of fertilization. Nitrogen addition neither resulted in a significant increase in forb cover, although it was expected, based on the results of other studies showing an increase in forb biomass in response to nitrogen fertilization (e.g. Walker & Knoop 1987; Seastedt *et al.* 1991). In contrast to numerous studies claiming that nutrients are involved in controlling herbaceous productivity (e.g. Roux & Warren 1963; Grunow *et al.* 1970; Van Andel & Van den Bergh 1987; Walker & Knoop 1987; Cohn *et al.* 1989; Scholes 1990; Belsky 1994; Knapp *et al.* 1998), we did not find nitrogen addition to significantly increase above-ground grass biomass after one season. To summarize, nitrogen addition had no significant effect on any parameter we measured. We ascribe the lack of significant results for species richness/diversity to a short study period rather than an insufficient level of nitrogen application (see 'Materials & Methods').

Fire

Fire also did not significantly affect any parameter in our study. This result is in accordance with Bowman *et al.* (1988) and a five-year study of Belsky's (1992), showing that fire had little effect on cover/dominance/diversity of grass species. We do not expect fire to be a major regulator of herbaceous composition and structure under ranching conditions in semi-arid savanna, because in the opinion of the local people, fuel loads are generally insufficient to support regular (and intense) fires, due to low rainfall and grazing (*cf.* Trollope 1982).

Interaction Effects

The field experiment yielded few significant interaction effects, although some trends occurred (these results are corroborated by results from a garden experiment, described in Chapter 2):

(1) Grazing *x* Nutrients:

Congruent with the results of Van Auken and Bush (1989), we found (in the garden experiment) a significant interaction between grazing (clipping) and nutrients (nitrogen) in its effect on grass biomass. The difference between clipped and unclipped plants was significantly larger under more favourable nitrogen levels. Note: due to the significant relationship between grass shoot biomass and light intensity we took the latter as an index of grass biomass.

(2) Rainfall *x* Nutrients:

The garden experiment showed a larger response of grass biomass to nitrogen addition under high rainfall, as was found by Walker and Knoop (1987) and Grunow *et al.* (1970). Similarly, the effects of rainfall were more pronounced under high nitrogen levels. By definition, water and nutrients are important limiting factors in semi-arid nutrient-poor savannas. Against this background of both water- and nitrogen-limitation, the interaction between rainfall and nitrogen is self-evident (Scholes 1990); with an increase in either one resource, production will still be restricted by the other limiting resource. Contrastingly, an increase in both will elicit a large response in terms of biomass production.

(3) Rainfall *x* Grazing:

Although not significant, our field experiment exhibited interaction between rainfall and grazing. Heavy grazing suppressed grass biomass production (and grass height) to a greater extent under high rainfall than low rainfall conditions. This result lends further support to our recommendation not to graze heavily in wet years (Chapter 2) if the aim is to maintain a competitive grass sward in order to prevent/minimize tree recruitment.

3.6   Conclusions

Very few grass parameters were affected by the treatments in our study, and site proved to be of overriding importance in determining herbaceous composition and structure. We generally ascribed the lack of significant results to a short study period in addition to the variation among sites. On this point, Belsky (1992) advised that one/two growing seasons (often used in similar studies) may not be long enough for many species to respond to treatments, and that three years may even be an inadequate response time in perennial herbaceous communities. She also showed that all grass parameters varied widely within treatments, years and sites, further justifying extensive and long-term studies. We would like to emphasize that this experiment was done within the framework of the overall study, which investigated tree-grass interactions, particularly during tree recruitment. Thus, the purpose of this experiment was to provide supplementary information to the overall study, rather than an in-depth investigation of the factors affecting savanna grass dynamics. We were aware that, for the latter, a longer study-period would have been more appropriate.

4. APPLYING A MECHANISTIC MODEL TO TREE-GRASS INTERACTIONS IN SEMI-ARID SAVANNAS

4.1 Abstract

The resource-ratio hypothesis or consumer-resource theory provides the basis for a state-space approach, demonstrating the dependence of community composition and richness on the availability of, and competition for limiting resources. Because equilibrium conditions are assumed, consumer-resource theory is open to criticism that equilibrium theory is often unsuitable to natural systems. We explored the applicability of consumer-resource theory to semi-arid nutrient-poor savannas. We also tested the explanatory power of consumer-resource theory for savannas against results from an experimental study investigating the effects of soil water status, nitrogen level and heavy grazing on *Acacia* tree recruitment. We demonstrated that consumer-resource theory facilitates the understanding of savanna functioning and enables qualitative predictions about changes in community structure in response to perturbing factors/processes. Consumer-resource theory should thus be particularly useful in understanding, predicting and managing bush encroachment. Contrary to many claims that equilibrium models are inappropriate for explaining savanna dynamics, we showed that consumer-resource theory has explanatory power for the savanna we studied. We infer that resource-competition plays a significant role in structuring the tree-grass communities of savannas.

Keywords: Tree-grass competition, consumer-resource theory, state-space approach, limiting resources, community structure.

4.2 Introduction

"The mission of community ecology... is to detect the *patterns* of natural systems, to explain them by discerning the causal *processes* that underlie them, and to generalize these explanations as far as possible."
(Wiens 1984)

There are many correlational, observational and experimental data sets which suggest that competition for resources plays a central role in structuring natural plant and animal communities (Walter 1971; Rapport & Turner 1975; Tilman 1982; Connell 1983; Schoener 1983; Paine 1984; Wilson & Keddy 1986; Goldberg & Barton 1992; Hughes et al. 1994; Ward & Seely 1996). As a consequence, a mechanistic understanding of community organization must incorporate the

differential ability of organisms to acquire and exploit limited resources (Real & Levin 1991). This work uses a broad definition of resources i.e. all factors consumed by a species and affecting its reproductive/growth rate are potentially limiting resources for it (Tilman 1982).

Tilman (1982) developed the consumer-resource approach to population ecology which he termed 'a theory of the structure and functioning of multispecies communities'. He presented a simple, graphical theory of multispecies competition for resources in order to demonstrate/predict the dependence of the species composition and richness of communities on the availability of limiting resources. This approach emphasizes the mechanisms of interactions among species and may be contrasted with the non-mechanistic approach of classical theory (e.g. the Lotka-Volterra model which did not consider how competition occurred, only its effects on population growth), although both use the graphical method of isoclines. The consumer-resource theory assumes that the interaction among species and between species with their environments are sufficiently strong as to establish major patterns which are discernible over noise. The competition resource theory is used to explore questions such as:

(1) How does resource competition predict which species will be dominant in a community and which will be rare?

(2) What limits does resource competition place on the diversity of a community?

(3) How do spatial structure and temporal variability influence species diversity?

(4) How may resource competition affect succession? (Tilman 1982)

The major driving forces in tree-grass dynamics in savannas are water, nutrients, fire and herbivory (Schultz *et al.* 1955; Frost *et al.* 1985; Knoop & Walker 1985; Van Auken *et al.* 1985; Walker & Knoop 1987; Stuart-Hill & Tainton 1988, 1989; Teague & Smit 1992; Jeltsch *et al.* 1996; Higgins *et al.* 2000). Water and nutrients are essential resources for which trees and grasses compete (Walter 1971; Walker & Noy-Meir 1982; Knoop & Walker 1985; O'Connor 1995), while disturbance (through fire and herbivory in the case of savannas) affects the availability of various essential resources (*viz.* light, space, water nutrients) (O'Connor 1985; Teague & Smit 1992) in addition to affecting the mortality (loss) rates of plant species (Trollope 1974, 1980; Roberts 1986). According to Scholes and Archer (1997), resource-partitioning patterns account for the observed patterns of primary production of trees and grasses in savannas. We explored the application of consumer-resource theory to tree-grass competition in semi-arid, nutrient-poor savannas of southern Africa. We assumed soil water and nitrogen to be the main limiting resources, because, by definition, semi-arid, nutrient-poor savannas are characterized by aridity and low nutrient levels. We demonstrate how this model simplifies and clarifies mechanistic understanding of tree-grass interaction in savannas in terms of resource competition between the tree and grass components.

We tested the predictive power of consumer-resource theory for savanna systems against results from an experimental study on tree recruitment in a grass matrix (Chapter 2). We also examined the potential of consumer-resource theory to open up new lines of thought on savanna dynamics as well as to identify possible approaches for future research.

4.3   Modelling Approach

Models are useful tools for understanding community processes in ecology and decision-making in conservation and land management (e.g. Shugart *et al.* 1973; Bart 1995; Dunning *et al.* 1995; Turner *et al.* 1995; Vance 1984; Jeltsch *et al.* 1996, 1997, 1998; Wiegand *et al.* 1999, 2000d; Joyce 2000; Keeling *et al.* 2000). A combination of short-term field investigations and pattern-oriented modelling (Grimm 1994) has the power to extract the maximum information available within a short-term study (Wiegand *et al.* 2000a), although it should not completely substitute for (long-term) field studies (Conroy *et al.* 1995) where long-term community dynamics are the issue at stake. An integrated approach (modelling and field studies) should promote both ecological knowledge of landscape phenomena and applications of landscape ecology to conservation and management (Conroy *et al.* 1995; Dunning *et al.* 1995; Wiegand *et al.* 1999). Because vegetation structure is critical to agricultural productivity (as in the case of livestock ranches in savannas), the ability to predict the consequences of possible management actions (within reasonable temporal and spatial bounds) is of fundamental importance (Teague & Smit 1992; Dunning *et al.* 1995; Turner *et al.* 1995).

The type of model to be used depends on the aim of the project and structure of the system (Fresco *et al.* 1987). The earliest (mathematical) population models were mainly based on Lotka-Volterra dynamics (Leslie 1945, 1948; Rosenzweig & MacArthur 1963; MacArthur & Levins 1967; Levine 1976) and very simplistic. These models did not describe the mechanism causing the observed result of, for example, competition or predation. Rather they described the outcome in terms of population size. Spatial models (combining a population simulator with the distribution of landscape features) are more complex and provide a mechanism for studying questions in vegetation dynamics, such as species-habitat relationships in space and time (Dunning *et al.* 1995; Turner *et al.* 1995). The visual nature of spatial models appeal to both land managers and researchers, thereby enhancing communication and making relevant information accessible to scientists and field managers (Turner *et al.* 1995). However, spatially-explicit models are often

individual-based (e.g. Jeltsch *et al.* 1996; Wiegand *et al.* 1999, 2000a,d,e; Higgins *et al.* 2000) implying that they are complex and have great data requirements (Wiegand *et al.* 1999), even more so when interspecific interactions are considered. Another form of individual-based models, so-called 'neighbourhood models', have also been used to describe and predict inter- and intraspecific competition among plants (Pacala & Silander 1985; Menaut *et al.* 1990; Silander & Pacala 1990). Keeping track of the precise neigbourhood of individuals is necessary only in certain instances (e.g. when individuals are clumped, and/or neighbour density is low/variable) (Silander & Pacala 1990), and thus not applicable to our system. Furthermore, these models are phenomenological, and thus have little predictive power in addition to having high data requirements and involving computationally intensive computer simulations (Morin 1999).

We chose Tilman's state-space approach (based on his consumer-resource theory), on account of it being mechanistic, therefore improving understanding of the mechanism involved in system processes and having predictive power. The approach is graphical and can be effectively used with either qualitative or quantitative information (*cf.* Jeltsch *et al.* 1996; Wiegand *et al.* 1999). This approach is further particularly suited to the scale (spatial and temporal) of population dynamics of interest, in contrast to individual-based models which require much more information and detail (see above), and models on forest succession covering centuries (e.g. Shugart *et al.* 1973). The model we used does not regard each individual plant, but rather the biomass of a population as a whole, which then serves as an index of the population's resource use, competitive ability, etc. For our purpose of considering tree-grass competition, this is particularly appropriate in light of variance between the encroaching tree species and grasses being much greater than among individual grasses. In the savanna we dealt with, grasses are not symbiotic N_2-fixers (Eisele *et al.* 1989; Brejda *et al.*1994), while the encroaching tree species (*Acacia mellifera* and all *Acacias*) is (Moshe *et al.* 2000). Grass species have a comparable growth form and grow faster than trees. Furthermore, grasses are negatively affected by heavy grazing (Ellison 1960; Du Toit 1972b; Van Auken & Bush 1989), whereas trees are not grazed by cattle or sheep. In summary, justification for using the state-space approach of Tilman's consumer-resource theory, was based on the structure of our system (trees *vs* grass-layer) and aim of this paper (*viz.* to make qualitative predictions about the way different factors affect tree-grass competition).

Lastly, we need to consider the controversy around equilibrium and stability, particularly in context of savannas, which are often regarded as transient/non-equilibrial systems (Ellis & Swift 1988; Skarpe 1992; Scholes & Walker 1993; Higgins *et al.* 2000). Paradigms in ecology have traditionally been divided into equilibrium and non-equilibrium models (Thompson 1987; Westoby *et al.* 1989; Seastedt & Knapp 1993). Tilman's consumer-resource theory is one of many

theories/models assuming that outcomes are resolved when equilibrium conditions are reached (Leslie 1945, 1948; Rosenzweig & MacArthur 1963; MacArthur & Levins 1967; Levine 1976). Is the use of equilibrium models appropriate, given many non-equilibrium systems/processes that have been described (Wiens 1977; McIntosh 1985; Westoby *et al.* 1989; Seastedt & Knapp 1993)? Importantly, all assessments of equilibrium/stability inevitably concern the scale, both spatial and temporal, at which we observe (Connell & Sousa 1983; DeAngelis & Waterhouse 1987). For example, savanna structure stays relatively constant when observed over long time periods (Menaut *et al.* 1990) and on a landscape scale, whereas conditions may differ greatly from one year to the next. However, variability over a short time-scale does not necessarily imply a shift away from equilibrium. On this point, Illius and O'Connor (1999) commented that "…stochastic variation leads to dynamics that might be confused with a non-equilibrial regime… and that …virtually all natural systems are to some extent non-equilibrial, if by this is meant that environmental fluctuations and stochastic variation are constantly redefining the equilibrium point. The fact that a system is not usually at equilibrium can merely obscure the operation of the underlying consumer-resource interactions: it is not itself evidence of the weakness of these interactions." Similarly, Scholes and Archer (1997) advised separating the issue of tree-grass coexistence in the long-term from resource partitioning in the short term, as the two may bear little relationship to one another. In response to criticism from Thompson (1987), Tilman (1987b) argued that his theory of resource competition is neither an equilibrium nor a non-equilibrium model. It rather is a theory of the mechanisms of plant competition, which can be solved mathematically to determine its 'equilibrium' predictions as well as its dynamics, including transient dynamics (e.g. succession). He further suggested that instead of expressing distinction between equilibrium and non-equilibrium theories, it is about approaches that investigate broad-scale, long-term patterns *vs* short-term dynamic responses of communites to perturbations. The larger scale and generality of Tilman's model matched our need for a model that would be easily extrapolatable to different sites and not limited to local situations under unique conditions.

4.4   Model Description

The following account of the model we used, is condensed from Tilman's consumer-resource theory (Tilman 1980, 1982, 1987b, 1988; Tilman & Pacala 1993). The model uses the conditions that exist once each population reaches equilibrium to predict the outcome of interspecific competition for resources. Four pieces of information are needed to predict the equilibrium outcome of resource competition:

    (1) the reproductive/growth (in terms of biomass) response of each species to the resources;

    (2) the mortality/loss rate experienced by each species;

    (3) the supply rate of each resource; and

    (4) the consumption rate of each resource by each species (Tilman 1982).

Competition for a Single Resource

In order to predict the outcome of competition for a single limiting resource, it is necessary to know the resource level at which the net rate of population change for a species is zero (i.e. the resource requirement of a species at equilibrium, R^*). R^* is represented by the environmental availability of a resource at which population change is zero (i.e. when gain (from reproduction and vegetative growth) just balance mortality/loss (from disturbance, predation, herbivory etc.)). The population size of a species will increase in a habitat where the actual resource level exceeds R^*, thereby reducing the resource level towards R^*. Conversely, if the resource level is less than R^*, the species' population size will decrease, allowing the resource level to increase because of decreased consumption rates. Only in habitats where resource levels are at R^*, will population size remain constant. R^* will increase with an increase in loss rate (Fig. 4.1), independent of the causes of losses (disturbance/predation/herbivory etc.), the number of species competing, and the competitive abilities of species in a habitat. When several species are all limited by a single resource, the one species with the lowest R^* is predicted to competitively displace all other species at equilibrium (e.g. Armstrong & McGehee 1980; Tilman 1988). The mechanism of competitive displacement is resource consumption. The population size of the species with the lowest R^* should be able to continue increasing until that species reduces the resource level down to its R^*, at which point there would be insufficient resource for the survival of the other species (Fig. 4.2). Thus, the species most efficient in exploiting the resource, i.e. able to survive at the lowest level of this resource, wins.
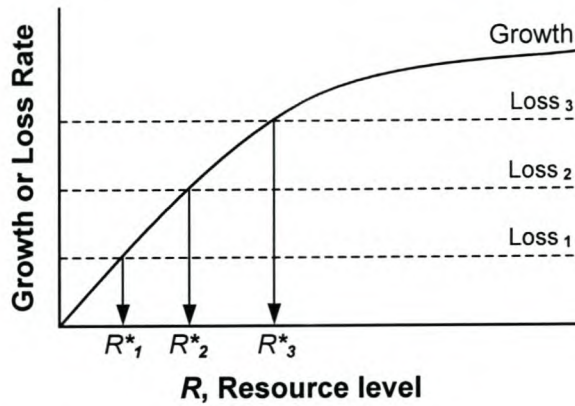
Figure 4.1: R^* is the environmental availability of a resource at which the population growth rate of a species (which is limited by the resource) is zero. Graphically, R^* is the resource level at which the growth rate and loss/mortality rate of the species balance. For a given growth rate, R^* increases (R^*_1 to R^*_3) with an increase in loss rate ($Loss_1$ to $Loss_3$).
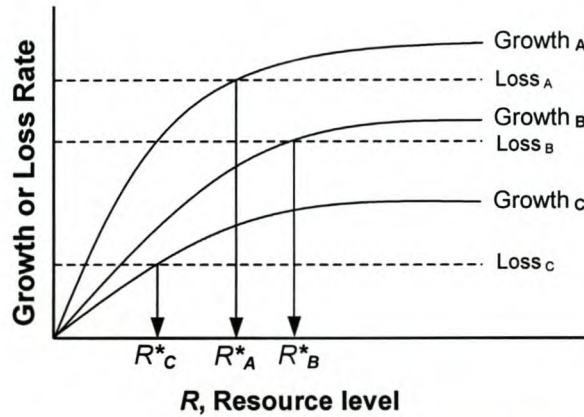

Figure 4.2: In a habitat where three species (A, B & C) are limited by the same resource, the species with the lowest R^* (species C in this case) will exclude the other two species in competition. (R^* is the resource level at which population growth rate is zero.) The increase in R^* with increasing loss rate (see Fig. 4.1) is a major element providing structure to habitats.

Competition for Two Resources

Resource-dependent Growth Isoclines

When a species consumes two or more resources, it is necessary to know the total effects of the resources on the growth rate of the species (Tilman 1988). Resource-dependent growth isoclines (so-called zero net growth isoclines, ZNGI) can be used to represent the resource requirements of a species at equilibrium (Tilman 1980, 1982) (Fig 4.3). These isoclines show all the combinations of concentrations of two essential resources for which a given species has a given growth rate

(Tilman 1980). Because reproductive rate increases with resource availability, isoclines further from the origin represent higher reproductive rates (Tilman 1982). Tilman (1982, 1988) discussed several types of resources. This paper only deals with essential resources, because the major resources involved in tree-grass competition are all essential (i.e. water, nitrogen and light) (*cf.* Roux 1969; Vitousek 1982; Tilman 1987b). Figure 4.3 shows isoclines for two resources which are essential with respect to each other. One essential resource is unable to substitute completely for another essential resource which is in low availability (thus, isoclines run parallel to both axes). If a habitat is at point x in Fig. 4.3, an increase in resource 1 (R_1) will not affect population size. However, any increase in resource 2 (R_2) will cause an increase in population size (and *vice versa* for a habitat at point y). ZNGIs with perfect right-angle corners (Fig. 4.3) assume that the plants are not plastic, but have independent fixed abilities to consume the two resources (Tilman 1988). However, physiological and morphological plasticity in plants leads to interactively-essential resource growth-isoclines which have a rounded corner (Fig. 4.4). Near the bend in the isocline, adding either R_1 or R_2 can lead to an increase in the population density of the species. Thus, there is dual limitation by both resources, which are functionally substitutable for each other over a range of resource levels. This is explained by the ability of a plant to modify its consumption such that a decrease in time/effort spent consuming one resource can allow an increase in the time/effort spent for consumption of the other (Tilman 1988). However, there is little qualitative difference, ecologically, between perfectly-essential and interactively-essential resources (Tilman 1982). Therefore, our conclusions will not be affected by whether we use perfectly- or interactively-essential resources.
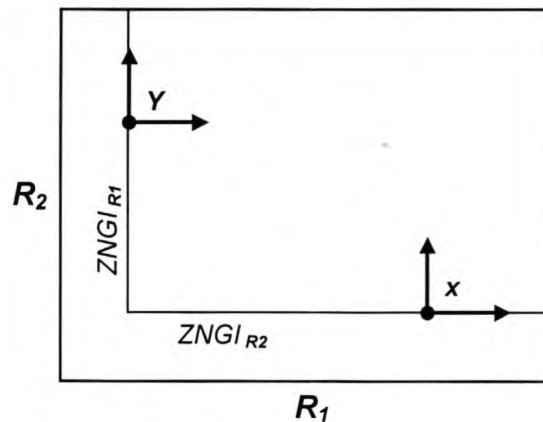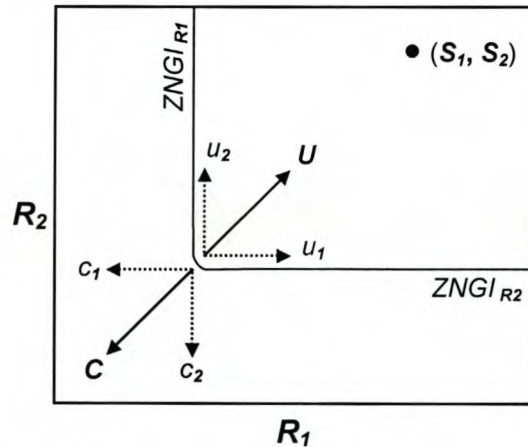

Figure 4.3: Zero net growth isoclines (ZNGI$_{R1}$ & ZNGI$_{R2}$) of a species, as limited by two essential resources (R_1 & R_2). Point x and y are two hypothetical habitats.

Resource Consumption & Resource Supply

Resource consumption needs to be considered because it affects subsequent resource availability. The resource consumption rates of each species can be represented as a vector (C) with two components (c_1 and c_2 in Fig. 4.4), each representing the consumption rate of one of the resources. c_1 is the amount of R_1 consumed per unit biomass of one species per unit time (and c_2 for R_2). The slope of the consumption vector thus indicates the proportional requirements of the two resources for a species.

We assume that each habitat has a particular, fixed resource supply point (S_1, S_2 in Fig. 4.4), which represents the maximal or total amounts of each resource that can exist in that particular habitat. We further assume that the rate of resource supply is proportional to the amount of that resource that is not currently in the available form (Tilman 1988). Similar to the resource consumption vector, a vector (pointing toward the supply point) can be drawn for the resource supply rate (U), with components for each of the resources' (R_1 and R_2) supply rates (u_1 and u_2 respectively) (Fig. 4.4). At equilibrium (i.e. zero population growth rate), the rate of resource consumption would equal the rate of resource supply. For a species to survive in a particular habitat, the supply point needs to be further from the origin than its ZNGI.


Figure 4.4: Population growth of one species limited by two essential resources (R_1 & R_2): zero net growth isoclines (ZNGI), the consumption vector (C), supply vector (U) and supply point (S_1, S_2).

Possible Outcomes to Interspecific Competition

There are three possible outcomes to two-species competition for two limiting resources: (a) either one of the species wins (Fig. 4.5a), (b) stable coexistence (Fig. 4.5b), or (c) unstable coexistence (Fig. 4.5c).

(a)   If one species (species A in Fig. 4.5a) has lower requirements for both R_1 and R_2 (i.e. when its ZNGI lies closer to the origin than that of species B), species A will outcompete B in all habitats in which both can survive.

(b)   There can only be a two-species equilibrium if the isoclines cross (this point is shown as a dot in Fig. 4.5b&c). The outcome of competition is determined by the ZNGIs in combination with the resource consumption vectors (C_A & C_B) of the two species. In Fig. 4.5b, species A, the superior competitor for R_1, is dominant in habitats in which both species are limited by R_1. In habitats with resource supply points for which both species are limited by R_2, species B, the superior competitor for R_2, wins. In intermediate habitats, each species is more limited by a different resource, and stably coexist. The coexistence is stable because each species consumes more of the resource that more limits it at equilibrium, i.e. intraspecific competition is stronger than interspecific competition (Connell 1983; Tilman 1988).

(c)   Unstable coexistence can result in intermediate habitats when each species consumes excess amounts of the resource that is most limiting to the other species (and not to itself) (Fig. 4.5c). Here, the outcome of competition will be determined by the initial conditions.

The closer the lines parallel to the resource consumption vectors of the two species are together, the smaller the increase in either limiting resource needed to move the system into a state of dominance by one species (and *vice versa*).
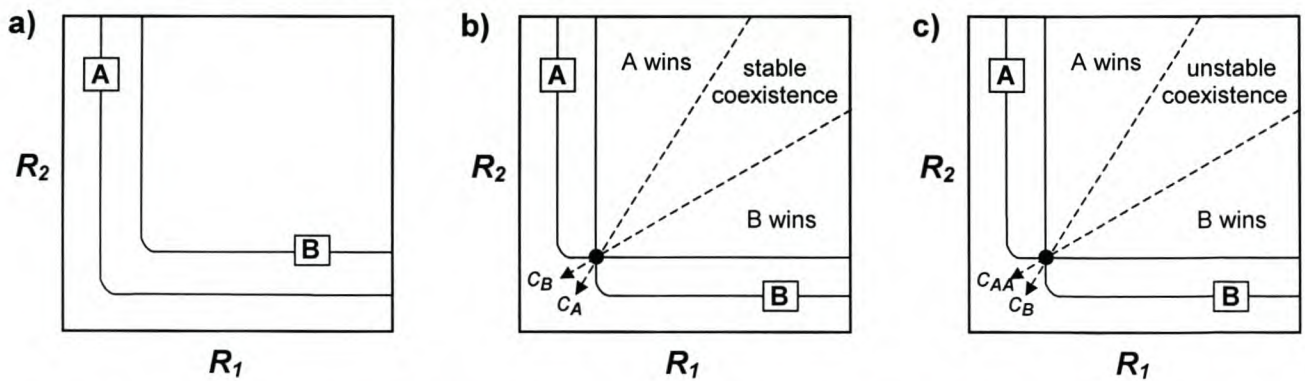
Figure 4.5: Possible outcomes for two species (A & B) in competition for two limiting resources (R_1 & R_2). Zero net growth isoclines (ZNGIs, solid lines) and consumption vectors (C_A & C_B, dotted lines) are shown for species A and B (at equilibrium). In **(a)** species A outcompetes species B in all habitats where both can survive, due to species A's lower resource requirements. Depending on the sector (as demarkated by ZNGIs and consumption vectors) in which a particular habitat (≈ resource levels) is situated, the outcome to competition in **(b)** may be dominance by either species or stable coexistence, while in **(c)** coexistence may be unstable or either species may dominate (see text for more detailed explanations).

4.5   Application to Savanna Systems

Disturbance

In the context of our study, disturbance may be caused by fire and grazing. Whatever the cause, disturbance in communities of sessile organisms can be thought of as a process that provides one or more required 80resource. For a plant community, the absence of other plants means that light, soil nutrients and water will be available for a colonist, in addition to the open space in which it can establish (Tilman 1982). An open site can thus be considered a composite resource, which encompasses the availability of numerous distinct resources associated with an unoccupied site. In most plant communities, the important qualities of an open site are probably the light and nutrient availabilities associated with the site, and not the open space (Tilman 1982). In semi-arid nutrient-poor savannas, water and nutrients should by definition be more limiting than light, while physical space should be least important because vegetation cover is generally low in dry areas. Dealing with space *per se* as a resource, is complicated by the fact that it is inseparable from the availability of other important limiting resources, e.g. soil water and nutrients. On this point, Tilman (1982) preferred to consider each resource (light, respective nutrients, water etc.) explicitly, rather than lumping these together in a summary variable (e.g. open site).

Particular Conditions

Throughout this section we considered the competitive interactions between *Acacia* trees and grasses (collectively – see 'Modelling approach'). We explored competition under the following conditions:

(1) limited and increased phosphorus and nitrogen;
(2) limited and increased soil water and soil nitrogen;
(3) fire prior to tree germination;
(4) heavy grazing; and
(5) heavy browsing.

(1) Phosphorus & Nitrogen

According to Liebig's law (Russell 1961), the yield potential of a plant is limited by the resource in shortest supply and yield can only be increased by increasing the levels of that particular resource. In general, nitrogen is the single most important soil nutrient for plant growth (Roux 1969; Vitousek 1982; Tilman 1987a) and only once requirements for nitrogen are met, will other nutrients (e.g. phosphorus) be limiting (Le Roux & Mentis 1986; Grunow *et al.* 1970). Grasses are often

limited by low soil nitrogen levels (Walker & Knoop 1987; Belsky 1994), while leguminous trees (such as of the genus *Acacia*) have the ability to fix atmospheric N_2 through symbiosis with bacteria (Schulze *et al.* 1991). Soil nitrogen is thus less limiting to the tree component than to the fast growing (non-leguminous) grasses. However, in phosphorus-deficient environments, such as the sandy soils of the Kalahari (southern Africa) (Donaldson & Kelk 1970), phosphorus becomes the most limiting nutrient to N_2-fixing trees. Such a scenario is illustrated in Fig. 4.6, showing the resource levels at which either trees or grasses will be dominant or stably coexist. As indicated by the arrows, an increase in phosphorus should shift the equilibrium in favour of the trees, while sufficient nitrogen supplementation should result in grass dominance.

(2) Water & Nitrogen

In competing for soil water and nitrogen (Fig. 4.7), tree seedlings are more limited by soil water (see Chapter 2) while grasses are more limited by soil nitrogen (because they are not N_2-fixing) (see above). The respective resource-limitations of trees and grasses explain the relative positions of their growth isoclines. An increase in soil water (during periods of above average rainfall) would temporarily favour tree seedlings, thereby creating favourable conditions for large-scale tree recruitment. Nitrogen addition, on the other hand, would give grasses a competitive advantage whereby tree recruitment could be suppressed. If both resources are increased at the same time to levels within the zone between the lines (C_G & C_T) parallel to the resource consumption vectors of the two species (Fig. 4.7), there would once again be stable coexistence.

(3) Fire prior to Tree Germination

Burning prior to tree germination affects the availability of several resources (soil water, soil nutrients, light and physical space) (Eisele *et al.* 1989; Breytenbach 1989; Blair *et al.* 1998) as well as the loss/mortality rate of grasses and tree recruits from previous years (Du Toit 1972a; Trollope 1974, 1980; Roberts 1986). Burning may either lead to an increase in soil moisture by reducing water consumption of grasses, or to a decrease in soil water through decreased water infiltration and increased evaporation from the now unvegetated soil surface (Teague & Smit 1992). Intense fires may change the soil characteristics (Breytenbach 1989), thereby altering water infiltration rates and ultimately soil water availability. Fire also affects nutrient availabilities in the soil; nitrogen losses have been ascribed to burning (Hobbs *et al.* 1991) but may again be significantly ameliorated by the stimulatory effect that phosphate, deposited in the ash following a fire, has on both symbiotic and associative N_2-fixation (Eisele *et al.* 1989; Blair *et al.* 1998). The nitrogen (and phosphate) status of N_2-fixing trees will thus be enhanced by fires, while nitrogen availability will be reduced for grasses. Burning further improves the availability of light and physical space for tree

germination. Although open space and improved light conditions may also benefit grasses, both these resources should be more critical to tree seedlings during early establishment than to the grass sward. Lastly, fire will affect the loss rate of both grasses and juvenile trees (within the flame zone) (Donaldson 1967b; Du Toit 1972a; Trollope 1974, 1980; Roberts 1986), thereby increasing the R^* of both components. However, if we only consider competition between newly emerged tree seedlings and the grass sward, R^* of only the grasses would be affected by fire.

Two possible scenarios as a result of pre-germination burning are graphically illustrated in Fig. 4.8a&b. Depending on the extent to which the ZNGI of the grass moves away from the origin (i.e. resource requirements increase as a result of a higher loss rate and higher R^*), there may still be scope for grass dominance (though unlikely) or tree-grass coexistence (Fig. 4.8a). Alternatively, trees may completely outcompete grasses (Fig. 4.8b). We emphasize that the destructive effect of fire on juvenile trees (more than a year old, but still within the flame zone) (Trollope 1974, 1980) will result in the opposite scenario by increasing the loss rate (and R^*) of trees relatively more than that of grasses (which are quicker to recover because they are fast-growing and because their resources are below-ground). The total effect of fire on the tree-grass ratio will thus be a trade-off between the positive influence of pre-germination fires on tree recruitment and the negative impact of post-germination fires on juvenile trees.

(4) Heavy Grazing

The effects of heavy grazing on tree-grass competition is similar to that of fire in many respects. Grazing reduces grass biomass (Van Auken & Bush 1989), thereby reducing water consumption by grasses and increasing soil moisture status. An increase in soil water availability will benefit tree seedlings more than grasses because trees are more limited by water than grasses (Fig. 4.9). However, there is a trade-off with water lost as a result of reduced infiltration (Kelly & Walker 1976) and high evaporation from a soil surface with less vegetation cover. The rate of nitrogen cycling (and therefore the nitrogen supply rate) is increased by grazing (Frank & Evans 1997; Holland & Detling 1990; Skarpe 1991; Holland *et al.* 1992), although this process is slow compared to other processes. An increase in soil nitrogen availability should favour grasses relatively more than tree seedlings, but, on the other hand, the loss rate of grasses is increased as a direct result of grazing. We expect that the latter effect will have a far greater impact than the slight increase in available nitrogen. The way light and space is affected by grazing is similar to that described for fire. If we assume that there is no net effect of grazing on soil water status due to the trade-off described above, grazing (overall) will benefit tree seedlings and retard grasses. If soil water is increased as a result of grazing, the beneficial effect on tree recruitment will be more pronounced. Conversely,

soil water levels may decrease as a result of increased runoff on bare patches (Snyman & Fouché 1991), which will negatively affect tree recruitment. The outcomes of heavy grazing would be similar to the two scenarios sketched for the effect of pre-germination fire, apart from the direction of change in nitrogen supply (*cf.* Fig. 4.8a & Fig. 4.9). The scenarios for grazing are presented in Fig. 4.8b & Fig. 4.9.
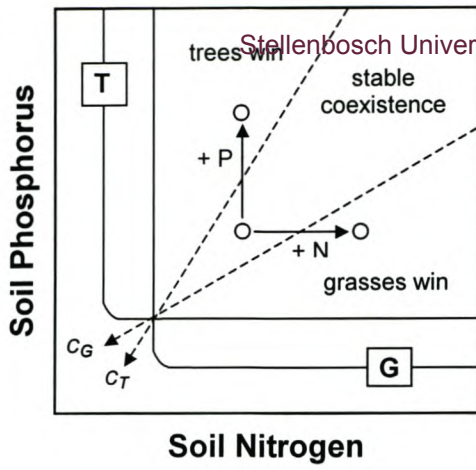
(5) Heavy Browsing

If trees are within reach of browsers, heavy browsing can significantly affect tree-grass competition (Du Toit 1972b; Teague 1986; Fierro *et al.* 1986; Stuart-Hill *et al.* 1987; Stuart-Hill & Tainton 1988, 1989). Smaller browsing ungulates usually concentrate on tree seedlings and new growth, thereby negatively affecting tree recruitment and establishment (Belsky 1984). Large browsers (e.g. elephant, black rhino, giraffe, eland and wildebeest) consume material from mature trees in addition to causing physical damage to woody growth (Spinage & Guinness 1971; Barnes 1983; Pellew 1983; Skarpe 1991). With regard to browsing, the tree component in our model (Fig. 4.10a&b) includes both seedlings and older trees. The main impact of heavy browsing should be an increase in the loss/mortality rate of the tree component (the R^* of trees will move away from the origin, Fig. 4.10a&b). The outcome of heavy browsing is thus opposite to that of heavy grazing and pre-germination fire. Once again, the degree of loss by trees will determine whether the system will go towards grass dominance in the extreme case (Fig. 4.10b) or whether tree-grass coexistence or tree dominance is possible. The effects of browsing on nutrient cycling and water status are not considered, because these are too slow compared to the effects of browsing mentioned.

Bush Encroachment

Bush encroachment can be seen as a particular outcome of tree-grass competition and an extreme state in community composition. The consumer-resource theory makes it clear that the ability to predict either the direction or the rate of change in community structure/composition depends on knowledge of the processes determining the budgets of various resources (Tilman 1982). Therefore, in order to understand, predict and prevent bush encroachment, we need to know how different processes (e.g. climatic variation) and disturbances (e.g. fire, grazing, browsing) affect resource dynamics, especially soil water and nitrogen, and competition for resources.

4.6) Soil Phosphorus vs Soil Nitrogen

4.7) Soil Water vs Soil Nitrogen

4.8a) Soil Water vs Soil Nitrogen

4.8b) Soil Water vs Soil Nitrogen

4.9) Soil Water vs Soil Nitrogen

4.10a) Soil Water vs Soil Nitrogen

4.10b) Soil Water vs Soil Nitrogen
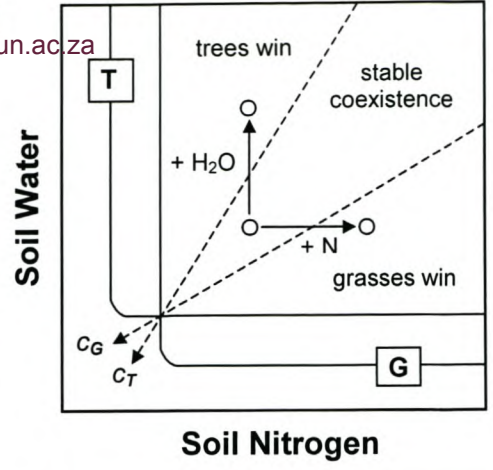
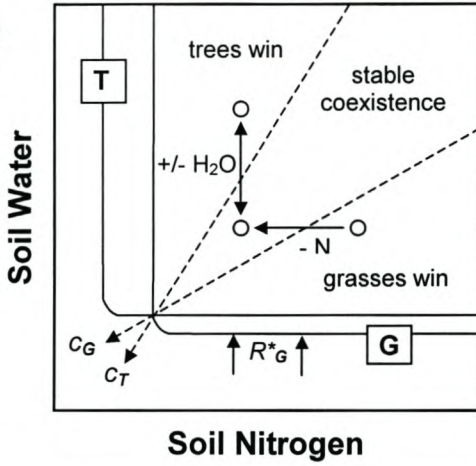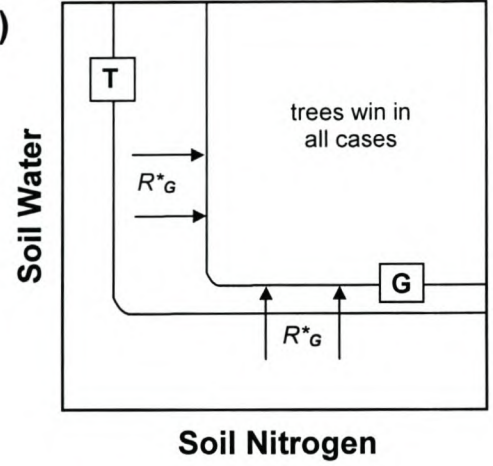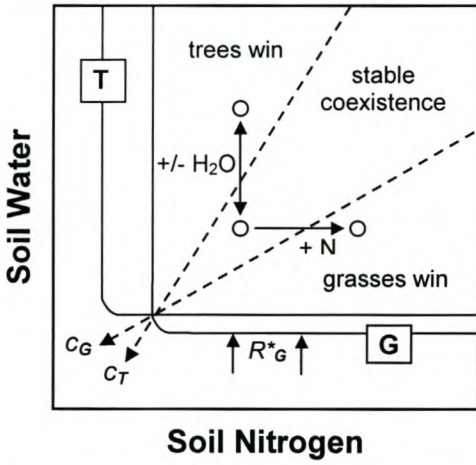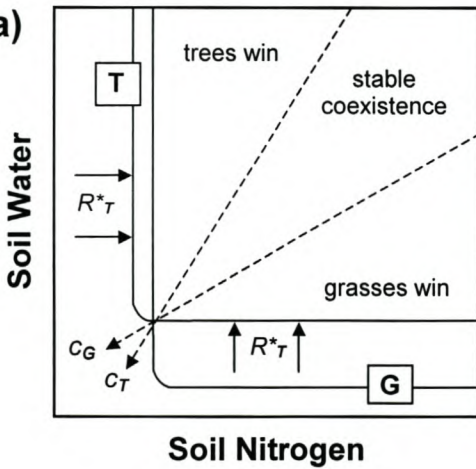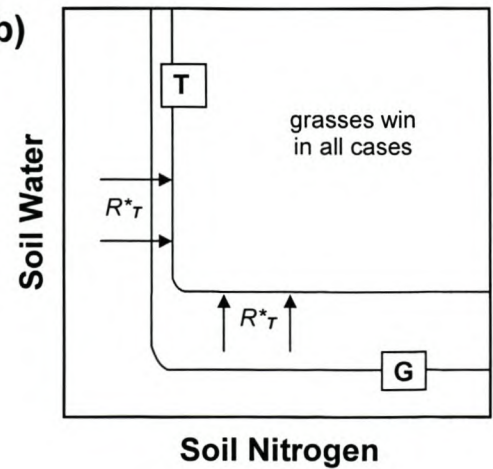**Figure 4.6:** The effects of limited and increased soil phosphorus (P) and soil nitrogen (N) on the abundances of *Acacia* trees (T) and grasses (G). An increase in phosphorus will favour trees, while an increase in nitrogen will favour grasses. The outcome of competition (stable coexistence or dominance by either trees or grasses) will depend on the level of resource increase relative to the position of both populations' growth isoclines and consumption vectors (C_T for trees & C_G for grasses).

Figure 4.7: The effects of limited and increased soil water and soil nitrogen (N) on the abundances of *Acacia* trees (T) and grasses (G). An increase in soil water will favour trees, while an increase in nitrogen will favour grasses. The outcome of competition will depend on the level of resource increase relative to the position of both populations' growth isoclines and consumption vectors (C_G & C_T).

Figure 4.8: Pre-germination fire can result in several outcomes. Fire increases the loss rate of grasses, thereby increasing the resource requirements of grasses (R^*_G) for maintenance of a given population biomass. In addition, fire alters the availability of soil water and nitrogen. The outcome of tree-grass competition in the event of pre-germination burning will therefore be a product of changes in resource levels and loss rates. Possible outcomes include **(a)** dominance by trees or grasses or coexistence; or **(b)** trees being the superior competitors at all resource levels at which both trees and grasses can exist.

Figure 4.9: Heavy grazing can affect tree-grass competition in several ways. Heavy grazing increases the loss rate of grasses, thereby increasing the resource requirements of grasses (R^*_G) for maintenance of a given population biomass. Grazing also affects the availability of soil water and nitrogen through altering consumption rates of these resources by grasses. In addition, reduced vegetation cover (due to grazing) may affect water infiltration and therefore soil water levels. Thus, the outcome of tree-grass competition under conditions of heavy grazing will be a product of changes in resource levels and loss rates. Possible outcomes include dominance by trees or grasses or coexistence (this figure); or trees being the superior competitors at all resource levels at which both trees and grasses can exist (Fig. 4.8b).

Figure 4.10: The effect of heavy browsing on competition between trees and grass for essential resources. Browsing increases the loss rate, and therefore the resource requirements (R^*_T) of trees. The extent to which browsing increases the trees' loss rate, will determine whether **(a)** dominance by either trees or grass, or tree-grass coexistence is possible; or whether **(b)** grasses will outcompete trees at all resource levels where both species can exist.

4.6   Model Validity

In order to examine the validity of Tilman's model for a particular system, one first needs to determine the levels of an essential resource at which the two competing species' respective growth curves asymptote (termed 'saturating' levels). The model is valid if increasing the resource to a point at/beyond the saturating levels for both species, moves that particular system in the direction predicted by the model. We tested the validity of Tilman's (1977, 1982, 1988) equilibrial resource-ratio model (i.e. consumer-resource theory) against our results from an experimental study that investigated the effects of various factors on tree recruitment in semi-arid savanna (Chapter 2), *viz.* the effects of (1) nitrogen addition; (2) high water levels; and (3) heavy grazing. With regard to these effects, the model's predictions can be summarized as follows (see 'Application to savanna systems' for a detailed explanation):

(1) sufficient nitrogen supplementation will result in grass dominance;

(2) an increase in soil water will create favourable conditions for large-scale tree recruitment; and

(3) given no nett effect of grazing on water status, heavy grazing will benefit tree seedlings and retard grasses.

(1) Nitrogen addition

Compared to controls, a large increase in nitrogen (which we assumed to be beyond the saturating point for grasses, because it was the highest level used by Tilman (1987a) in North American grasslands) significantly increased grass growth and depressed tree germination. Thus, these results matched the model's predictions.

(2) High water levels

Water addition (again to a level higher than ever experienced in the field) significantly enhanced tree recruitment compared to the control treatment, although grass growth also benefited from the water addition. In order to predict the outcome of competition between tree seedlings and grass, we would have had to quantify the beneficial effect of high water levels on each component in comparable terms (which we were not able to do). However, the model still was not falsified by our results, because the effect of high water levels on tree recruitment corresponded to the direction of change predicted by the model, even though grass performance was also affected. A limitation to this garden experiment was the short study period (one growing-season) and the small spatial scale (one experimental unit was 0.16 m^2), which did not allow monitoring of tree-grass interaction until later developmental stages, which would have been more indicative of the outcome of competition.

(3) Heavy grazing

Regular clipping of grasses resulted in higher tree germination and higher tree seedling biomass, compared to unclipped treatments. Therefore clipping (≈grazing) indirectly benefited tree seedlings by incurring a cost to the grasses, making the latter less competitive for the limiting resources (as predicted by the model).

4.7   Conclusions

We attempted to improve our understanding of species coexistence and competition, in particular within the context of savannas. The consumer-resource model we used makes qualitative predictions about community structure, based on information about limiting essential resources. Consequently, our results support Tilman's (1982) claims on the importance of resource competition in structuring natural plant communities. The model further enabled us to conceptualize and explain the principles underlying savanna dynamics. By using a state-space approach, we could explore how different factors/disturbances affect tree-grass competition without requiring detailed prior information. Complexity is minimized in the model by treating competing populations as biomass rather than individuals, and by the generality of incorporating loss – whether it is caused by grazing, browsing or fire – as an increase in R^* (resource requirement at zero population change/equilibrium). Contrary to many claims that equilibrium concepts/models are inappropriate for explaining savanna dynamics (Ellis & Swift 1988; also see review by DeAngelis & Waterhouse 1987), we showed that Tilman's resource-ratio equilibrium model has explanatory power for the semi-arid nutrient-poor savannas we studied. The utility of the model is enhanced by its qualitative and large-scale approach, making it easily extrapolable to different sites and under various conditions. Indeed, it is the generality and mechanistic basis of the resource-ratio models that makes them so useful in community ecology.

The output of a model depends not only on the assumed relations and mathematical equations, but also on the parameter values used (Thalen *et al.* 1987; Bart 1995; Conroy *et al.* 1995; Ruckelshaus *et al.* 1997). If specific quantitative output is required for an individual system, other approaches, e.g. individual-based models, may be more suitable, but for our purpose of generality, the state-space approach was suitable. Future research could improve the ability of the model to make specific predictions for particular situations by obtaining quantitative information on the exact positions of ZNGIs. Furthermore, separate models could be built, considering the interaction

between trees and each grass species individually, to determine if these yield results comparable to those when grasses are treated collectively. At this stage we believe it was premature to add such complexity. The level of difference between trees and grasses in growth habits is so large compared to the difference among grasses that we could retain generality by treating the grasses collectively.

Our controlled, multi-factor field and garden experiments, investigating several treatments and their interactions (Chapter 2), meshed well with a modelling approach, and helped us to understand the mechanisms involved in savanna dynamics and structure. Various environmental perturbations and/or management actions could be included in the model to generate predictions, which could then be experimentally tested by applying these perturbations as treatments in a research protocol. Such a combined approach should provide both understanding about system functioning and feedback for improving management (Conroy *et al.* 1995). In conclusion, we believe our approach contributed towards the 'mission of community ecology', *viz.* to detect patterns of natural systems, discern causal processes, and generalize explanations as far as possible (*cf.* Wiens 1984).

GENERAL CONCLUSIONS

Despite the large spatial extent of savannas and several decades of research, the dynamics of these systems are not well understood (Jeltsch *et al.* 2000). Because the structure of savanna vegetation has considerable economical implications for various agricultural industries, proper knowledge of system functioning is essential. In particular, bush encroachment, as a specific outcome of tree-grass competition in savannas, and cause of serious losses in livestock production and biodiversity, needs be understood to be effectively managed.

Bush encroachment is a complex phenomenon (Wiegand *et al.* 2000c). An unequivocal explanation/ solution to bush encroachment may not be feasible due to the vast number of interaction possibilities between factors that may provide ideal recruitment conditions in heterogeneous savanna systems (in time, space and land-use history). For this reason, Donaldson (1967a) advised not to attempt finding a universal solution to bush encroachment. However, in order to develop a comprehensive picture of the system under study we need to understand the influence of single factors (Wiegand *et al.* 2000c). Our completely-crossed, multi-factorial and replicated experiments (Chapter 2) were particularly suited for this purpose. We investigated the effects of various factors and their interactions on the initial stages of bush encroachment (i.e. germination and early survival). Our experiments adhered to the recommendations of Goldberg and Barton (1992) for studying species interactions and competition effectively, in which they emphasized the need for complex, multi-factor designs and including analyses of interaction terms.

In summary, we found that an extreme rainfall amount is insufficient to cause bush encroachment, while frequent rain (i.e. constant water availability) was the single most important factor initiating large-scale *Acacia mellifera* recruitment. Given that rainfall conditions were adequate, nitrogen addition retarded bush encroachment while grazing increased it, grazing being the least important of these three factors. We believe the results we obtained for *A. mellifera* to be extrapolable to other semi-arid nutrient-poor savannas. The manner in which rainfall, nitrogen and grazing affected tree-grass dynamics in our study, should be applicable to other water- and nitrogen-limited systems where the tree component is partly made up by leguminous tree species (i.e. including the majority of African savannas dominated by *Acacia* species (Du Toit 1995; Van Wilgen & Scholes 1997) and large parts of North-American savannas dominated by *Prosopis* species (Archer 1989)). One could expect species-specific responses of the tree component to shade (as a function of grass biomass and thus grazing) and fire, in that tree species may be shade-tolerant or -intolerant (e.g. Bush & Van Auken 1990; O'Connor 1995) and differ in their abilities (as seeds/seedlings/juveniles/mature trees) to survive and recover from fire (e.g. Babalwa & Witkowski 1997; see also Table 1.1).

Our results on tree germination and early survival, provided an ecological basis for formulating management recommendations relevant to the prevention of the initiation of bush encroachment:

(1) Because large-scale tree recruitment should only occur in above-average rainfall seasons, managers in semi-arid areas prone to bush encroachment should reduce stocking rates in wet years to a level that minimizes the creation of bare patches by grazing in order to reduce the probability that tree recruitment can occur. In other words, the competitive ability of grasses against trees should be maximimized especially in wet years, (in the formulation of Tilman (Chapter 4) to reduce loss and thus keep R* for grasses as low as possible). This is contrary to traditional thinking, which advocates that care should mainly be taken not to overstock in dry years. However, we do not advocate overstocking in dry years, because this can retard grass cover and competitive ability in the long term, but emphasize the importance of low grazing intensity in years of above-average rainfall.

(2) Nitrogen-poor environments are more prone to bush encroachment by leguminous tree species. Again, farmers should take extra care not to overexploit grasses on nitrogen-poor soils, as nitrogen-limitation already places grasses at a disadvantage relative to the tree component.

The experimental period of this study neglected dry season and post first season seedling survival. As a result, management recommendations focused on the prevention of mass tree recruitment. A study covering several growing seasons could establish whether later stages of woody encroachment could also be managed according to these recommendations.

Although the main aim of this study was not an in-depth investigation of grass dynamics *per se*, the results obtained for different grass parameters were essential for:

(1) identifying initial differences between sites (i.e. historical effects);

(2) establishing the magnitude of historical effects relative to treatment effects; and

(3) proper understanding of tree-grass competition, as influenced by the way treatments affect grass competitive ability.

Furthermore, these results lend support to general trends in the literature (e.g. the effects of grazing on grass performance) and revealed interesting interaction effects.

The integration of an experimental and modelling approach enhanced our understanding of the mechanisms operating in the system under study. Importantly, a dimension of predictive ability was added to this study – our results had extended value due to its general applicability as demonstrated by the model's predictions. The model, being rooted in consumer-resource theory, meshed well with the experimental treatments, which involved direct/indirect manipulation of levels of the most limiting resources. The simplicity and graphical nature of the model have the potential

to facilitate understanding of system processes by field managers. The combined approach also allows for evaluating management actions and providing feedback in order to improve range management (Conroy *et al.* 1995).

To summarize, we believe this study contributed towards understanding of savanna dynamics and more specifically, the early stages of bush encroachment. We identified ideal conditions for large-scale *Acacia mellifera* recruitment, *viz.* high rainfall frequency, nitrogen-poor soils and low grass biomass, and established the relative importance of each of these factors. Our diverse approach (incorporating field and garden experiments and modelling) embodied progress in the search for general patterns, understanding of system processes and attaining the ability to predict and evaluate the consequences of possible management actions (*cf.* Wiens 1984), which are all essential to planning and problem-solving at the ranch level (Teague & Smit 1992).

Adding to the diverse approach of this study is its being part of a broader and longer-term project that aims to acquire holistic understanding of the system studied on which to base guidelines for sustainable management of semi-arid savannas. The issues addressed by the overarching project at Pniel Estates include:

(1) ascertaining if bush encroachment by *A. mellifera* is limited by seed availability;

(2) experimenting with the timing of rainfall to determine its relation to *A. mellifera* recruitment;

(3) establishing whether/how the vegetation has changed by comparing historical records (oral and written records and aerial photographs) with current ecological assessments;

(4) determining the extent of bush encroachment in the area and its influence on cattle/game farming and biodiversity conservation;

(5) understanding the genetic factors underlying the distribution of the main encroaching species (*A. mellifera*) in the area;

(6) assessing the effects of different management types (commercial and communal farming with game, cattle or mixed stock) on soil quality; and

(7) determining sustainable stocking rates for communal and commercial rangelands by relating diet quantity and quality to the nutritional constraints of animals.

By addressing many gaps in our knowledge of savannas, this project should contribute greatly to wise and informed management of these ecosystems.

REFERENCES

Ackerman JD, Sabat A & Zimmerman JK. 1996. Seedling establishment in an epiphytic orchid: an experimental study of seed limitation. *Oecologia* 106:192-198.

Acocks JPH. 1988. Veld types of South Africa. *Memoirs of the Botanical Survey of South Africa* 57:1-146.

Adams ME. 1967. A study of the ecology of *Acacia mellifera, A. seyal* and *Balanites aegyptiaca* in relation to land-clearing. *Journal of Applied Ecology* 4:221-237.

Alef K. & Nannipieri P. 1995. *Methods in applied soil microbiology and biochemistry.* Academic Press, London.

Anderson LJ, Brumbaugh MS & Jackson RB. 2001. Water and tree-understory interactions: a natural experiment in a savanna with oak wilt. *Ecology* 82:33-49.

Andersson CJ. 1856. *Lake Ngami: on explorations and discoveries, during four years' wanderings in the wilds of south western Africa.* Hurst and Blackett, London.

Archer S. 1989. Have southern Texas savannas been converted to woodlands in recent history? *The American Naturalist* 134:545-561.

Archer S. 1996. Assessing and interpreting grass-woody plant dynamics. In *The ecology and management of grazing systems*, Hodgson J & Illius AW (Eds.), pp. 101-134. CAB International, Wallingford.

Archer S, Scifres C, Bassham CR & Maggio R. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecological Monographs* 58:111-127.

Armstrong RA & McGehee. 1980. Competitive exclusion. *The American Naturalist* 115:151-170.

Aucamp AJ, Barnard HH & Venter JJ. 1981. Beef cattle and Boer goat performances in the dry grass-bush communities of the Eastern Cape. *Proceedings of the Grassland Society of Southern Africa* 16:45-48.

Aucamp AJ, Danckwerts JE, Teague WR & Venter JJ. 1983. The role of *Acacia karroo* in the False Thornveld of the Eastern Cape. *Proceedings of the Grassland Society of Southern Africa* 18:151-154.

Babalwa AM & Witkowski ETF. 1997. Tolerance to soil temperatures experienced during and after the passage of fire in seeds of *Acacia karroo, Acacia tortilis* and *Chromolaena odorata*. *South African Journal of Botany* 63:421-425.

Barnes PW & Archer S. 1996. Influence of an overstorey tree (*Prosopis glandulosa*) on associated shrubs in a savanna parkland: implications for patch dynamics. *Oecologia* 105:493-500.

Barnes RFW. 1983. Effects of elephant browsing on woodlands in a Tanzanian National Park: measurements, models and management. *Journal of Applied Ecology* 20:521-540.

Bart J. 1995. Acceptance criteria for using individual-based models to make management decisions. *Ecological Applications* 5:411-420.

Bate GC, Furniss PR & Pendle BG. 1982. Water relations of southern African savannas. In *Ecology of tropical savannas*, Ecological studies Vol. 42, Huntley BJ & Walker BH (Eds.), pp. 336-358. Springer-Verlag, New York.

Bazzaz FA. 1990. The response of natural ecosystems to the rising global CO_2 levels. *Annual Review of Ecology and Systematics* 21:167-196.

Bazzaz FA & Harper JL. 1976. Relationship between plant weight and numbers in mixed populations of *Sinapis alba* (L.) Rabenh. and *Lepidium sativum* L. *Journal of Applied Ecology* 13:211-216.

Becker LH (Ed.). Undated. *Report on the economic utilization of densifying bush species in Namibia.* Ministry of Trade and Industry, Namibia.

Belsky AJ. 1984. Role of small browsing mammals in preventing woodland regeneration in the Serengeti National Park, Tanzania. *African Journal of Ecology* 22:271-279.

Belsky AJ. 1986. Does herbivory benefit plants? A review of the evidence. *The American Naturalist* 127:870-892.

Belsky AJ. 1992. Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *Journal of Vegetation Science* 3:187-200.

Belsky AJ. 1994. Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. *Ecology* 75:922-932.

Belsky AJ, Amundson RG, Duxbury JM, Riha SJ, Ali AR & Mwonga SM. 1989. The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. *Journal of Applied Ecology* 26:1005-1024.

Belsky AJ, Carson WP, Jensen CL & Fox GA. 1993a. Overcompensation by plants: herbivore optimization or red herring? *Evolutionary Ecology* 7:109-121.

Belsky AJ, Mwonga SM, Amundson RG, Duxbury JM & Ali AR. 1993b. Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. *Journal of Applied Ecology* 30:143-155.

Belsky AJ, Mwonga SM & Duxbury JM. 1993c. Effects of widely spaced trees and livestock grazing on understory environments in tropical savannas. *Agroforestry Systems* 24:1-20.

BenDavid-Novak H & Schick AP. 1997. The response of *Acacia* tree populations on small alluvial fans to changes in the hydrological regime: Southern Negev Desert, Israel. *Catena* 29:341-351.

Berendse F. 1979. Competition between plant populations with different rooting depths. *Oecologia* 43:19-26.

Berkowitz AR, Canham CD & Kelly VR. 1995. Competition *vs.* facilitation of tree seedling growth and survival in early successional communities. *Ecology* 76:1156-1168.

Bezuidenhout H. 1994. An ecological study of the major vegetation communities of the Vaalbos National Park, Northern Cape. 1. The Than-Droogeveld section. *Koedoe* 37:19-42.

Bezuidenhout H. 1995. An ecological study of the major vegetation communities of the Vaalbos National Park, Northern Cape. 2. The Graspan-Holpan section. *Koedoe* 38:65-83.

Billé JC. 1985. Some aspects of bush encroachment in the African rangelands. In *International savanna symposium 1984*, Tothill JC & Mott JC (Eds.), pp. 213-216. Globe Press Pty Ltd, Victoria.

Blackburn WH & Tueller PT. 1970. Pinyon and juniper invasion in black sagebrush communities in east-central Nevada. *Ecology* 51:841-848.

Blair JM, Seastedt TR, Rice CW & Ramundo RA. 1998. Terrestrial nutrient cycling in tallgrass prairie. In *Grassland dynamics. Long-term ecological research in tallgrass prairie*, Knapp AK, Briggs JM, Hartnett DC & Collins SL (Eds.), pp. 222-243. Oxford University Press, Oxford.

Bond WJ & Van Wilgen BW. 1996. Fire and plants. Population and community biology series 14. Chapman & Hall, London.

Booth CA. 1986. The effect of microtopography and woollybutt (*Eragrostis eriopoda*) competition on the survival of hopbush (*Dodonaea attenuata*) seedlings. In *Rangelands: a resource under siege. Proceedings of the Second International Rangeland Congress* (Adelaide 1985), pp. 32-33. Cambridge University Press, Cambridge.

Booth WE. 1941. Revegetation of abandoned fields in Kansas and Oklahoma. *American Journal of Botany* 28:415-422.

Borchert MI, Davis FW, Michaelsen J & Oyler LD. 1989. Interactions of factors affecting seedling recruitment of blue oak (*Quercus douglasii*) in California. *Ecology* 70:389-404.

Bosch OJH & Van Wyk JJP. 1970. The influence of bushveld trees on the productivity of *Panicum maximum*: a preliminary report. *Proceedings of the Grassland Society of Southern Africa* 5:69-74.

Bosch PJA. 1993. *Geological survey: The geology of the Kimberley area. Explanation of sheet 2824. Scale 1:250 000.* Department of Mineral and Energy Affairs, Republic of South Africa. Government Printer, Pretoria.

Bowman DMJS, Wilson BA & Hooper RJ. 1988. Response of *Eucalyptus* forest and woodland to four fire regimes at Munmarlary, Northern Territory, Australia. *Journal of Ecology* 76:215-232.

Boyd RS. 1988. Microdistribution of the beach plant *Cakile maritima* (Brassicaceae) as influenced by a rodent herbivore. *American Journal of Botany* 75:1540-1548.

Bradstock RA & Auld TD. 1995. Soil temperatures during experimental bushfires in relation to fire intensity: consequences for legume germination and fire management in south-eastern Australia. *Journal of Applied Ecology* 32:76-84.

Brejda JJ, Kremer RJ & Brown JR. 1994. Indications of associative nitrogen fixation in eastern gamagrass. *Journal of Range Management* 47:192-196.

Breytenbach GJ. 1989. Alien control: can we afford to slash and burn Hakea in fynbos ecosystems? *South African Forestry Journal* 151:6-16.

Brown JR & Archer S. 1987. Woody plant seed dispersal and gap formation in a North American subtropical savanna woodland: the role of domestic herbivores. *Vegetatio* 73:73-80.

Brown JR & Archer S. 1989. Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. *Oecologia* 80:19-26.

Brown JR & Archer S. 1999. Shrub invasion of grassland: recruitment is continuous and not regulated by herbaceous biomass or density. *Ecology* 80:2385-2396.

Buffington LC & Herbel CH. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. *Ecological Monographs* 35:139-164.

Burrows WH, Beale IF, Silcock RG & Pressland AJ. 1985. Prediction of tree and shrub population changes in a semi-arid woodland. In *International savanna symposium 1984*, Tothill JC & Mott JC (Eds.), pp. 207-211. Globe Press Pty Ltd, Victoria.

Bush JK & Van Auken OW. 1990. Growth and survival of *Prosopis glandulosa* seedlings associated with shade and herbaceous competition. *Botanical Gazette* 151:234-239.

Bush JK & Van Auken OW. 1995. Woody plant growth related to planting time and clipping of a C_4 grass. *Ecology* 76:1603-1609.

Caldwell MM & Richards JH. 1989. Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. *Oecologia* 79:1-5.

Caldwell MM, Richards JH, Manwaring JH & Eissenstat DM. 1987. Rapid shifts in phosphate acquisition show direct competition between neighbouring plants. *Nature* 327:615-616.

Callaway RM & Walker LR. 1997. Competition and facilitation: a synthetic approcah to interactions in plant communities. *Ecology* 78:1958-1965.

Campbell QP, Ebersöhn JP & Von Broembsen HH. 1962. Browsing by goats and its effects on the vegetation. *Herbage Abstracts* 32:273-275.

Carr JD. 1976. *The South African Acacias*, pp.242-245. Conservation Press, Johannesburg.

Chalk PM. 1991. The contribution of associative and symbiotic nitrogen fixation to the nitrogen nutrition of non-legumes. *Plant and Soil* 132:29-39.

Chirara C, Frost PGH & Gwarazimba VEE. 1999. Grass defoliation affecting survival and growth of seedlings of *Acacia karroo*, an encroaching species in southwestern Zimbabwe. *African Journal of Range and Forage Science* 15:41-47.

Cohen J. 1988. *Statistical power analysis for the behavioral sciences* (2nd ed.). Lawrence Erlbaum Associates Publishers, New Jersey.

Cohn EJ, Van Auken OW & Bush JK. 1989. Competitive interactions between *Cynodon dactylon* and *Acacia smallii* seedlings at different nutrient levels. *The American Midland Naturalist* 121:265-272.

Collins SL & Steinauer EM. 1998. Disturbance, diversity, and species interactions in tallgrass prairie. In *Grassland dynamics. Long-term ecological research in tallgrass prairie*, Knapp AK, Briggs JM, Hartnett DC & Collins SL (Eds.), pp. 140-156. Oxford University Press, Oxford.

Condon RW. 1986a. Scrub invasion on semi-arid grazing lands in western New South Wales – causes and effects. In *Rangelands: a resource under siege. Proceedings of the Second International Rangeland Congress* (Adelaide 1985), pp. 40. Cambridge University Press, Cambridge.

Condon RW. 1986b. Financial and other benefits from goats on scrub (brush)-infested semi-arid rangelands in western New South Wales. In *Rangelands: a resource under siege. Proceedings of the Second International Rangeland Congress* (Adelaide 1985), pp. 235-236. Cambridge University Press, Cambridge.

Connell JH. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *The American Naturalist* 122:661-696.

Connell JH & Sousa WP. 1983. On the evidence needed to judge ecological stability or persistence. *The American Naturalist* 121:789-824.

Conroy MJ, Cohen Y, James FC, Matsinos YG & Maurer BA. 1995. Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. *Ecological Applications* 5:17-19.

Cook CW & Stubbendieck J (Eds.). 1986. *Range research: basic problems and techniques*. Society of Range Management, Broomfield, USA.

Cooper SM. 1982. The comparative feeding behaviour of goats and impalas. *Proceedings of the Grassland Society of Southern Africa* 17:117-121.

Coutinho LM. 1982. Ecological effect of fire in Brazilian Cerrado. In *Ecology of tropical savannas*, Ecological studies Vol. 42, Huntley BJ & Walker BH (Eds.), pp. 273-291. Springer-Verlag, New York.

Crawley MJ & Rees M. 1996. The balance of plant populations. In *Frontiers of population ecology*, Floyd RB, Sheppard AW & De Barro PJ (Eds.), pp. 191-212. CSIRO Publishing, Melbourne.

Cresswell CF, Ferrar P, Grunow JO, Grossman D, Rutherford MC & Van Wyk JJP. 1982. Phytomass, seasonal phenology and photosynthetic studies. In *Ecology of tropical savannas*, Ecological studies Vol. 42, Huntley BJ & Walker BH (Eds.), pp. 476-497. Springer-Verlag, New York.

Cumming DHM. 1982. The influence of large herbivores on savanna structure in Africa. In *Ecology of tropical savannas*, Ecological studies Vol. 42, Huntley BJ & Walker BH (Eds.), pp. 215-245. Springer-Verlag, New York.

Dart P, Umali-Garcia M & Almendras A. 1991. Role of symbiotic associations in nutrition of tropical acacias. In *Advances in tropical acacia research, ACIAR Proceedings No. 35*, Turnbull JW (Ed.), pp. 13-19.

Davis MA, Wrage KJ & Reich PB. 1998. Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. *Journal of Ecology* 86:652-661.

Dean WRJ. 1992. Effects of animal activity on the absorption rate of soils in the southern Karoo, South Africa. *Journal of the Grassland Society of Southern Africa* 9:178-180.

Dean WRJ & Macdonald IAW. 1994. Historical changes in stocking rates of domestic livestock as a measure of semi-arid and arid rangeland degradation in the Cape Province, South Africa. *Journal of Arid Environments* 26:281-298.

Dean WRJ, Milton SJ & Jeltsch F. 1999. Large trees, fertile islands, and birds in arid savanna. *Journal of Arid Environments* 4:61-78.

DeAngelis DL & Waterhouse JC. 1987. Equilibrium and nonequilibrium concepts in ecological models. *Ecological Monographs* 57:1-21.

Donaldson CH. 1966. Control of Blackthorn in the Molopo area with special reference to fire. *Proceedings of the Grassland Society of Southern Africa* 1:57-62.

Donaldson CH. 1967a. *Bush encroachment with special reference to the Blackthorn problem of the Molopo area*. Department of Agricultural Technical Services, Armoedsvlakte Research Station, Vryburg.

Donaldson CH. 1967b. Further findings on the effects of fire on Blackthorn. *Proceedings of the Grassland Society of Southern Africa* 2:59-61.

Donaldson CH. 1978. Evaluation of *Cenchrus ciliaris*: II. A comparison of bushveld, de-bushed veld and bushveld combined with *Cenchrus* pastures. *Proceedings of the Grassland Society of Southern Africa* 13:45-48.

Donaldson CH & Kelk DM. 1970. An investigation of the veld problems of the Molopo area: I. Early findings. *Proceedings of the Grassland Society of Southern Africa* 5:50-57.

Downing BH. 1978. Environmental consequences of agricultural expansion in South Africa since 1850. *South African Journal of Science* 74:420-422.

Dukes JS & Mooney HA. 1999. Does global change increase the success of biological invaders? *Tree* 14:135-139.

Dunning JB, Stewart DJ, Danielson BJ, Noon TL, Lamberson RH & Stevens EE. 1995. Spatially explicit population models: current forms and future uses. *Ecological Applications* 5:3-11.

Du Toit JT. 1995. Determinants fo the composition and distribution of wildlife communitites in southern Africa. *Ambio* 24:2-6.

Du Toit PF. 1968. A preliminary report on the effect of *Acacia karroo* competition on the composition and yield of sweet grassveld. *Proceedings of the Grassland Society of Southern Africa* 3:147-149.

Du Toit PF. 1972a. *Acacia karroo* intrusion: the effect of burning and sparing. *Proceedings of the Grassland Society of Southern Africa* 7:23-27.

Du Toit PF. 1972b. The goat in a bush-grass community. *Proceedings of the Grassland Society of Southern Africa* 7:44-50.

Dye PJ & Spear PT. 1982. The effects of bush clearing and rainfall variability on grass yield and composition in south-west Zimbabwe. *Zimbabwe Journal of Agricultural Research* 20:103-118.

Eisele KA, Schimel DS, Kapustka LA & Parton WJ. 1989. Effects of available P and N:P ratios on non-symbiotic dinitrogen fixation in tallgrass prairie soils. *Oecologia* 79:471-474.

Ellis JE & Swift DM. 1988. Stability of African pastoral ecosystems: alternate paradigms and implications for development. *Journal of Range Management* 41:450-459.

Ellison L. 1960. Influence of grazing on plant succession of rangelands. *The Botanical Review* 26:1-78.

Emanuel WR, Shugart HH & Stevenson MP. 1985a. Climatic change and the broad-scale distribution of terrestrial ecosystem complexes. *Climatic Change* 7:29-43.

Emanuel WR, Shugart HH & Stevenson MP. 1985b. Response to comment: climatic change and the broad-scale distribution of terrestrial ecosystem complexes. *Climatic Change* 7:457-460.

Eriksen FI & Whitney AS. 1981. Effects of light intensity on growth of some tropical forage species. I. Interaction of light intensity and nitrogen fertilization on six forage grasses. *Agronomy Journal* 73:427-433.

Ernst WHO. 1988. Seed and seedling ecology of *Brachystegia spiciformis*, a predominant tree component in miombo woodlands in South Central Africa. *Forest Ecology and Management* 25:195-210.

Fierro LC, Gomez F, Gonzalez MH & Chavez A. 1986. Use of goats to increase forage and animal production in brush infested rangelands of northern Mexico. In *Rangelands: a resource under siege. Proceedings of the Second International Rangeland Congress* (Adelaide 1985), pp. 254-255. Cambridge University Press, Cambridge.

Fowler N. 1982. Competition and coexistence in a North Carolina grassland. III. Mixtures of component species. *Journal of Ecology* 70:77-92.

Frank DA & Evans RD. 1997. Effects of native grazers on grassland N cycling in Yellowstone National Park. *Ecology* 78:2238-2248.

Fresco LFM, Van Laarhoven HPM, Loonen MJJE & Moesker T. 1987. Ecological modelling of short-term plant community dynamics under grazing with and without disturbance. In *Disturbance in grasslands*, Van Andel J, Bakker JP & Snaydon RW (Eds.), pp. 149-165. Kluwer Academic Publishers Group, Dordrecht.

Frost PGH. 1985. Organic matter and nutrient dynamics in a broadleafed African savanna. In *International savanna symposium 1984*, Tothill JC & Mott JC (Eds.), pp. 200-206. Globe Press Pty Ltd, Victoria.

100

Frost P, Medina E, Menaut JC, Solbrig O, Swift M & Walker B (Eds.). 1985. Responses of savannas to stress and disturbance. *Biology International* 10:1-82.

Frost WE & McDougald NK. 1989. Tree canopy effects on herbaceous production of annual rangeland during drought. *Journal of Range Management* 42:281-283.

Gammon DM. 1983. Effects of bush clearing, stocking rates and grazing systems on vegetation and cattle gains in the south western lowveld of Zimbabwe. *Zimbabwe Agriculture Journal* 80:219-228.

Garcia-Moya E & McKell CM. 1970. Contribution of shrubs to the nitrogen economy of a desert-wash plant community. *Ecology* 51:81-88.

Goldberg DE & Barton AM. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *The American Naturalist* 139:771-801.

Grime JP. 1979. *Plant strategies and vegetation processes.* Wiley, Chichester.

Grimm V. 1994. Mathematical models and understanding in ecology. *Ecological Modelling* 75/76:641-651.

Grunow JO. 1980. Feed and habitat preferences among some large herbivores on African veld. *Proceedings of the Grassland Society of Southern Africa* 15:141-146.

Grunow JO, Pienaar AJ & Breytenbach C. 1970. Long term nitrogen application to veld in South Africa. *Proceedings of the Grassland Society of Southern Africa* 5:75-90.

Harrington GN. 1991. Effects of soil moisture on shrub seedling survival in a semi-arid grassland. *Ecology* 72:1138-1149.

Harrington GN & Hodgkinson KC. 1986. Shrub-grass dynamics in mulga communities of eastern Australia. In *Rangelands: a resource under siege. Proceedings of the Second International Rangeland Congress* (Adelaide 1985), pp. 26-28. Cambridge University Press, Cambridge.

Hayashi I. 1992. A preliminary report of an experiment on vegetation recovery of drought deciduous woodland in Kitui, Kenya. *African Journal of Ecology* 30:1-9.

Heady HA. 1975. *Rangeland management.* McGraw-Hill, New York.

Higgins SI, Bond WJ & Trollope WSW. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* 88:213-229.

Hobbs NT, Schimel DS, Owensby CE & Ojima DS. 1991. Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. *Ecology* 72:1374-1382.

Hobbs RJ & Mooney HA. 1986. Community changes following shrub invasion of grasslands. *Oecologia* 70:508-513.

Hoffman MT & O'Connor TG. 1999. Vegetation change over 40 years in the Weenen/Muden area, KwaZulu-Natal: evidence from photo-panoramas. *African Journal of Range and Forage Science* 16:71-88.

Hoffman MT, Cowling RM, Douie C & Pierce SM. 1989. Seed predation and germination of *Acacia erioloba* in the Kuiseb River Valley, Namib Desert. *South African Journal of Botany* 55:103-106.

Hoffman MT, Todd SW, Ntshona Z & Turner SD. 1999. *A national review of land degradation in South Africa. Chapter 7. Vegetation degradation.* National Botanical Institute of South Africa Web Site. [online]. Available from: http://www.nbi.ac.za/landdeg/ [Accessed 1st February 2002].

Holland EA & Detling JK. 1990. Plant response to herbivory and belowground nitrogen cycling. *Ecology* 71:1040-1049.

Holland EA, Parton WJ, Detling JK & Coppock DL. 1992. Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow. *The American Naturalist* 140:685-706.

Holmgren M, Scheffer M & Huston MA. 1997. The interplay of facilitation and competition in plant communities. *Ecology* 78:1966-1975.

Holt JA & Coventry RJ. 1990. Nutrient cycling in Australian savannas. *Journal of Biogeography* 17:427-432.

Holz G & Schreuder W. 1989. Dieback of blackthorn (*Acacia mellifera* subsp. d*etinens*) in South West Africa. *Agricola* 7:32-36.

Hughes JJ, Ward D & Perrin MR. 1994. Predation risk and competition affect habitat selection and activity of Namib desert gerbils. *Ecology* 75:1397-1405.

Illius AW & O'Connor TG. 1999. On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. *Ecological Applications* 9:798-813.

Janse van Rensburg H. 1939. A further contribution to the ecology of the Highveld grassland at Frankenwald, in relation to grazing. *South African Journal of Science* 36:238-245.

Janzen DH. 1982. Removal of seeds from horse dung by tropical rodents: influence of habitat and amount of dung. *Ecology* 63:1887-1900.

Jarvel LC & O'Connor TG. 2000. Bushclump-grass interactions: influence of bushclumps on their local environment in a south-east African savanna. *African Journal of Range & Forage Science* 16:32-43.

Jeltsch F, Milton SJ, Dean WRJ & Van Rooyen N. 1996. Tree spacing and coexistence in sermiarid savannas. *Journal of Ecology* 84:583-595.

Jeltsch F, Milton SJ, Dean WRJ & Van Rooyen N. 1997. Analysing shrub encroachment in the southern Kalahari: a grid-based modelling approach. *Journal of Applied Ecology* 34:1497-1508.

Jeltsch F, Milton SJ, Dean WRJ, Van Rooyen N & Moloney KA. 1998. Modelling the impact of small-scale heterogeneities on tree-grass coexistence in semi-arid savannas. *Journal of Ecology* 86:780-793.

Jeltsch F, Weber GE & Grimm V. 2000. Ecological buffering mechanisms in savannas: A unifying theory of long-term tree-grass coexistence. *Plant Ecology* 150:161-171.

Johnson HB, Polley HW & Mayeux HS. 1993. Increasing CO_2 and plant-plant interactions: effects on natural vegetation. *Vegetatio* 104/105:157-170.

Joubert JGV. 1966. Die invloed van verskillende behandelings op die verhouding van Swarthaak tot gras in die Damaralandse doringboomsavanne in Suidwes-Afrika. *Annals of the University of Stellenbosch* 41A(9):433-463.

Joyce LA. 2000. From equations to understanding. *Rangelands* 22:40-44.

Kanz WA. 2001. *Seed and seedling dynamics of certain Acacia species as affected by herbivory, grass competition, fire, and grazing system.* MSc Thesis, University of Natal.

Keeling MJ, Wilson HB & Pacala SW. 2000. Reinterpreting space, time lags, and functional responses in ecological models. *Science* 290:1758-1761.

Kelk DM & Donaldson CH. 1970. An investigation of veld problems in the Molopo area: II. Some practical implications or the experimental findings. *Proceedings of the Grassland Society of Southern Africa* 5:58-61.

Kellman M. 1979. Soil enrichment by neotropical savanna trees. *Journal of Ecology* 67:565-577.

Kelly RD & Walker BH. 1976. The effects of different forms of land use on the ecology of a semi-arid region of south-eastern Rhodesia. *Journal of Ecology* 64:553-576.

Knapp AK, Briggs JM, Blair JM & Turner CL. 1998. Patterns and controls of aboveground net primary production in tallgrass prairie. In *Grassland dynamics. Long-term ecological research in tallgrass prairie*, Knapp AK, Briggs JM, Hartnett DC & Collins SL (Eds.), pp. 193-221. Oxford University Press, Oxford.

Knoop WT & Walker BH. 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. *Journal of Ecology* 73:235-253.

Kramer PJ. 1981. Carbon dioxide concentration, photosynthesis, and dry matter production. *BioScience* 31:29-33.

Krebs CJ. 1989. *Ecological methodology.* Harper & Row, New York.

Kreuter UP, Archer SR & Scifres CJ. 1999. Bio-economic basis for woody plant management. In *Proceedings of the Sixth International Rangeland Congress*, Vol. 2, pp. 842-843. VI International Rangeland Congress Inc., Queensland.

Lacey CJ, Walker J & Noble IR. 1982. Fire in Australian tropical savannas. In *Ecology of tropical savannas*, Ecological studies Vol. 42, Huntley BJ & Walker BH (Eds.), pp. 246-272. Springer-Verlag, New York.

Lay DW. 1965. Effects of periodic clipping on yield of some common browse species. *Journal of Range Management* 18:181-184.

Lenzi-Grillini CR, Viskanic P & Mapesa M. 1996. Effects of 20 years of grazing exclusion in an area of the Queen Elizabeth National Park, Uganda. *African Journal of Ecology* 34:333-341.

Le Roux NP & Mentis MT. 1986. Veld compositional response to fertilization in the tall grassveld of Natal. *South African Journal of Plant and Soil* 3:1-10.

Leslie PH. 1945. On the use of matrices in certain population mathematics. *Biometrika* 33:183-212.

Leslie PH. 1948. Some further notes on the use of matrices in certain population mathematics. *Biometrika* 35:213-245.

Levine SH. 1976. Competitive interactions in ecosystems. *The American Naturalist* 110:903-910.

Levy EB & Madden EA. 1933. The point method of pasture analysis. *New Zealand Journal of Agriculture* 46:267-279.

Louda SM, Keeler HH & Holt RD. 1990. Herbivore influences on plant performance and competitive interactions. In *Perspectives on plant competition*, Grace JB & Tilman D. (Eds.), pp. 414-444. Academic Press, New York.

Low AB & Rebelo ATG (Eds.). 1998. *Vegetation of South Africa, Lesotho and Swaziland.* Department of Environmental Affairs and Tourism, Pretoria.

Low WA, Miller C & Potts R. 1999. Establishment of vegetation on mine waste dumps in the Tanami Desert, central Australia. In *Proceedings of the Sixth International Rangeland Congress*, Vol. 2, pp. 979-981. VI International Rangeland Congress Inc., Queensland.

MacArthur R & Levins R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist* 101:377-385.

Machlis L & Torrey JG. 1956. *Plants in action: a laboratory manual of plant physiology*, p. 36. WH Freeman & Company Inc., San Francisco.

Madany MH & West NE. 1983. Livestock grazing-fire regime interactions within montane forests of Zion National Park, Utah. *Ecology* 64:661-667.

Magnuson JJ. 1990. Long-term ecological research and the invisible present. *Bioscience* 40:495-501.

Maher C. 1945. The goat: friend or foe? *East African Agricultural Journal* 11:115-121.

McIntosh RP. 1985. *The background of ecology*. Cambridge University Press, Cambridge.

McNaughton SJ. 1979a. Grassland-herbivore dynamics. In *Serengeti: dynamics of an ecosystem*, Sinclair ARE & Norton-Griffiths M (Eds.), pp. 46-81. University of Chicago Press, Chicago.

McNaughton SJ. 1979b. Grazing as optimization process: grass-ungulate relationships in the Serengeti. *The American Naturalist* 113:691-703.

McNaughton SJ. 1984. Grazing lawns: animals in herds, plant form, and coevolution. *The American Naturalist* 124:863-886.

McNaughton SJ. 1986. Grazing lawns: on domesticated and wild grazers. *The American Naturalist* 128:937-939.

McPherson GR & Wright HA. 1990. Effects of cattle grazing and *Juniperus pinchotii* canopy cover on herb cover and production in western Texas. *The American Midland Naturalist* 123:144-151.

McPherson GR, Boutton TW & Midwood AJ. 1993. Stable carbon isotope analysis of soil organic matter illustrates vegetation change at the grassland/woodland boundary in southeastern Arizona, USA. *Oecologia* 93:95-101.

Medina E. 1982a. Nitrogen balance in the Trachypogon grasslands of Central Venezuela. *Plant and Soil* 67:305-314.

Medina E. 1982b. Physiological ecology of neotropical savanna plants. In *Ecology of tropical savannas*, Ecological studies Vol. 42, Huntley BJ & Walker BH (Eds.), pp. 308-335. Springer-Verlag, New York.

Medina E & Silva JF. 1990. Savannas of northern South America: a steady state regulated by water-fire interactions on a background of low nutrient availability. *Journal of Biogeography* 17:403-413.

Menaut JC, Gignoux J, Prado C & Clobert J. 1990. Tree community dynamics in a humid savanna of the Côte-d'Ivoire: modelling the effects of fire and competition with grass and neighbours.

Midgley GF, Bond WJ, Roberts R & Wand SJE. 1998. Will Gullivers travel? Potential causes of changes in savanna tree success due to rising atmospheric CO_2. In *Towards sustainable management in the Kalahari region. Some essential background and critical issues. Proceedings of Kalahari Transect Workshop*, Ringrose S & Chanda R (eds.), pp. 166-175. Directorate of Research and Development, University of Botswana, Gaborone.

Miller MF & Coe M. 1993. Is it advantageous for *Acacia* seeds to be eaten by ungulates? *Oikos* 66:364-368.

Mills PFL. 1964. Effects of fertilizer on the botanical composition of veld grassland at Matopos. *Rhodesia Agriculture Journal* 61:91-93.

Milton SJ. 1980. *Studies on Australian Acacias in the south western Cape, South Africa*. MSc Thesis, University of Cape Town.

Milton SJ. 1987. Phenology of seven *Acacia* species in South Africa. *South African Journal of Wildlife Research* 17:1-7.

Milton SJ & Dean WRJ. 1995. South Africa's arid and semiarid rangelands: why are they changing and can they be restored? *Environmental Monitoring and Assessment* 37:245-264.

Milton SJ, Dean WRJ, Du Plessis MA & Siegfried WR. 1994. A conceptual model of arid rangeland degradation. *BioScience* 44:70-76.

Miranda CHB & Boddey RM. 1987. Estimation of biological nitrogen fixation associated with 11 ecotypes of *Panicum maximum* grown in nitrogen-15-labeled soil. *Agronomy Journal* 79:558-563.

Morin PJ. 1999. *Community Ecology*, pp. 29-66. Blackwell Science Inc., London.

Morris DR, Zuberer DA & Weaver RW. 1985. Nitrogen fixation by intact grass-soil cores using $^{15}N_2$ and acetylene reduction. *Soil Biology and Biochemistry* 17:87-91.

Moshe D, Bailey CL & Scholes RJ. 2000. The effect of elevated atmospheric carbon dioxide on selected savanna plants. In *Towards sustainable management based on scientific understanding of natural forests and woodlands. Proceedings: Natural forests and savanna woodlands symposium II*, Seydack AHW, Vermeulen WJ & Vermeulen C (Eds.), pp. 142-144. Department of Water Affairs and Forestry, Knysna, South Africa.

Mueller-Dombois D & Ellenberg H. 1974. *Aims and methods of vegetation ecology*. Wiley, New York.

Munzbergova Z & Ward D. 2001, in press. *Acacia* trees as keystone species in Negev desert ecosystems. *Journal of Vegetation Science*.

Nielson RP. 1986. High-resolution climatic analysis and southwest biogeography. *Science* 232:27-34.

Norton-Griffiths M. 1979. The influence of grazing, browsing and fire on the vegetation dynamics of the Serengeti. In *Serengeti: dynamics of an ecosystem*, Sinclair ARE & Norton-Griffiths M (Eds.), pp. 310-352. University of Chicago Press, Chicago.

Noy-Meir I & Walker BH. 1986. Stability and resilience in rangelands. In *Rangelands: a resource under siege. Proceedings of the Second International Rangeland Congress* (Adelaide 1985), pp. 21-25. Cambridge University Press, Cambridge.

Obeid M & Seif El Din A. 1970. Ecological studies of the vegetation of Sudan. I. *Acacia senegal* (L.) Willd. and its natural regeneration. *Journal of Applied Ecology* 7:507-518.

O'Connor TG. 1985. A synthesis of field experiments concerning the grass layer in the savanna regions of southern Africa. *South African National Scientific Programmes Report No 114*. Foundation for Research Development, CSIR, Pretoria.

O'Connor TG. 1991. Local extinction in perennial grasslands: a life-history approach. *The American Naturalist* 137:753-773.

O'Connor TG. 1993. The influence of rainfall and grazing on the demography of some African savanna grasses: a matrix modelling approach. *Journal of Applied Ecology* 30:119-132.

O'Connor TG. 1994. Composition and population responses of an African savanna grassland to rainfall and grazing. *Journal of Applied Ecology* 31:155-171.

O'Connor TG. 1995. *Acacia karroo* invasion of grassland: environmental and biotic effects influencing seedling emergence and establishment. *Oecologia* 103:214-223.

O'Connor TG & Crow VRT. 2000. Rate and pattern of bush encroachment in Eastern Cape savanna and grassland. *African Journal of Range and Forage Science* 16:26-31.

O'Connor TG & Pickett GA. 1992. The influence of grazing on seed production and seed banks of some African savanna grasslands. *Journal of Applied Ecology* 29:247-260.

Owen-Smith N. 1993. Woody plants, browsers and tannins in southern African savannas. *South African Journal of Science* 89:505-510.

Owen-Smith N & Cooper SM. 1985. Comparative consumption of vegetation components by kudus, impalas and goats in relation to their commercial potential as browsers in savanna regions. *South African Journal of Science* 81:72-76.

Pacala SW & Silander JA. 1985. Neighborhood models of plant populations dynamics. I. Single-species models of annuals. *The American Naturalist* 125:385-411.

Pakeman RJ & Hay E. 1996. Heathland seedbanks under bracken *Pteridium aquilinum* (L.) Kuhn and their importance for revegetation after bracken control. *Journal of Environmental Management* 47:329-339.

Palgrave KC. 1977. *Trees of Southern Africa*. Struik, Cape Town.

Palmer AR, Crook BJS & Lubke RA. 1988. Aspects of the vegetation and soil relationships in the Andries Vosloo Kudu Reserve, Cape Province. *South African Journal of Botany* 54:309-314.

Palmer E & Pitman N. 1972. *Trees of Southern Africa*, Vol. 2, pp. 750-753. AA Balkema, Cape Town.

Paine RT. 1984. Ecological determinism in the competition space. *Ecology* 65:1339-1348.

Pellew RAP. 1983. The impacts of elephant, giraffe and fire upon the *Acacia tortilis* woodlands of the Serengeti. *African Journal of Ecology* 21:41-74.

Perkins JS & Thomas DSG. 1993. Spreading deserts or spatially confined impacts? Land degradation and cattle ranching in the Kalahari desert of Botswana. *Land Degradation and Rehabilitation* 4:179-194.

Peterman RM. 1990. The importance of reporting statistical power: the forest decline and acidic deposition example. *Ecology* 71:2024-2027.

Pianka ER & Huey RB. 1971. Bird species density in the Kalahari and the Australian deserts. *Koedoe* 14:123-129.

Pitt MD, Newman RF, Youwe PL, Wikeem BM & Quinton DA. 1998. Using a grazing pressure index to predict cattle damage of regenerating tree seedlings. *Journal of Range Management* 51:417-422.

Potter CS. 1992. Stemflow nutrient inputs to soil in a successional hardwood forest. *Plant and Soil* 140:249-254.

Rapport DJ & Turner JE. 1975. Feeding rates and population growth. *Ecology* 56:942-949.

Real LA & Levin SA. 1991. Theoretical advances. The role of theory in the rise of modern ecology. In *Foundations of ecology. Classic papers with commentaries*, Real LA & Brown JH (Eds.), pp. 177-191. University of Chicago Press, Chicago.

Rice CW, Todd TC, Blair JM, Seastedt TR, Ramundo RA & Wilson GWT. 1998. Belowground biology and processes. In *Grassland dynamics. Long-term ecological research in tallgrass prairie*, Knapp AK, Briggs JM, Hartnett DC & Collins SL (Eds.), pp. 244-264. Oxford University Press, Oxford.

Roberts BR. 1985. Stability in savanna lands. In *International savanna symposium 1984*, Tothill JC & Mott JC (Eds.), pp. 195-196. Globe Press Pty Ltd, Victoria.

Roberts BR. 1986. A comparison of Southern African and Australian grazing management recommendations. In *Rangelands: a resource under siege. Proceedings of the Second International Rangeland Congress* (Adelaide 1985), pp. 219-221. Cambridge University Press, Cambridge.

Rohner C & Ward D. 1997. Chemical and mechanical defense against herbivory in two sympatric species of desert Acacia. *Journal of Vegetation Science* 8:717-726.

Rohner C & Ward D. 1999. Large mammalian herbivores and the conservation of arid *Acacia* stands in the Middle East. *Conservation Biology* 13:1162-1171.

Rosenzweig M. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385-387.

Rosenzweig ML & MacArthur RH. 1963. Graphical representation and stability conditions of predator-prey interactions. *The American Naturalist* 97:209-223.

Ross JH. 1979. A conspectus of the African *Acacia* species. *Memoirs of the Botanical Survey of South Africa*, No. 44, pp. 65-67.

Roux ER. 1969. Grass, a story of Frankenwald. Oxford University Press, Cape Town.

Roux P. 1966. Die uitwerking van seisoensreënval en beweiding op gemengde karooveld. *Proceedings of the Grassland Society of Southern Africa* 1:103-110.

Roux ER & Middlemiss E. 1963. The occurrence and distribution of *Acacia cyanoplylla* and *A. cyclops* in the Cape Province. *South African Journal of Science* 59:286-294.

Roux ER & Warren M. 1963. Plant succession on abandoned fields in central Oklahoma and in the Transvaal highveld. *Ecology* 44:576-579.

Ruckelshaus M, Hartway C & Kareiva P. 1997. Assessing the data requirements of spatially explicit dispersal models. *Conservation Biology* 11:1298-1306.

Russell EW. 1961. *Soil conditions and plant growth.* Longmans, Green & Co Ltd, London.

Russell GE, Watson L, Koekemoer M, Smook L, Barker NP, Anderson HM & Dallwitz MJ. 1991. Grasses of southern Africa. *Memoirs of the Botanical Survey of South Africa*, No. 58. Botanical Research Institute, Pretoria.

Rutherford MC & Panagos MD. 1982. Seasonal woody plant shoot growth in *Burkea africana-Ochna pulchra* savanna. *South African Journal of Botany* 1:104-116.

Salihi DO & Norton BE. 1987. Survival of perennial grass seedlings under intensive grazing in semi-arid rangelands. *Journal of Applied Ecology* 24:145-151.

Samarakoon SP, Wilson JR & Shelton HM. 1990. Growth, morphology and nutritive quality of shaded *Stenotaphrum secundatum, Axonopus compressus* and *Pennisetum clandestinum. Journal of Agricultural Science* 114:161-169.

Samuels ML. 1989. *Statistics for the life sciences.* Dellen Publishing Company, San Francisco.

Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA & Whitford WG. 1990. Biological feedbacks in global desertification. *Science* 247:1043-1048.

Schoener TW. 1983. Field experiments on interspecific competition. *The American Naturalist* 122:240-285.

Scholes RJ. 1990. The influence of soil fertility on the ecology of southern African dry savannas. *Journal of Biogeography* 17:415-419.

Scholes RJ & Archer SR. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* 28:517-544.

Scholes RJ & Walker BH. 1993. *An African savanna. Synthesis of the Nylsvley study.* Cambridge University Press, Cambridge.

Schultka W & Cornelius R. 1997. Vegetation structure of a heavily grazed range in northern Kenya: tree and shrub canopy. *Journal of Arid Environments* 36:290-306.

Schultz AM, Launchbauch JL & Biswell HH. 1955. Relationship between grass density and brush seedling survival. *Ecology* 36:226-238.

Schulze E-D, Gebauer G, Ziegler H & Lange OL. 1991. Estimates of nitrogen fixation by trees on an aridity gradient in Namibia. *Oecologia* 88:451-455.

Scott JD. 1967. Bush encroachment in South Africa. *South African Journal of Science* 63:311-314.

Seastedt TR & Knapp AK. 1993. Consequences of nonequilibrium resource availability across multiple time scales: the transient maxima hypothesis. *The American Naturalist* 141:621-633.

Seastedt TR, Briggs JM & Gibson DJ. 1991. Controls of nitrogen limitation in tallgrass prairie. *Oecologia* 87:72-79.

Seastedt TR, Hayden BP, Owensby CE & Knapp AK. 1998. Climate change, elevated CO_2, and predictive modeling. Past and future climate change scenarios for the tallgrass prairie. In *Grassland dynamics. Long-term ecological research in tallgrass prairie*, Knapp AK, Briggs JM, Hartnett DC & Collins SL (Eds.), pp. 283-300. Oxford University Press, Oxford.

Shackleton CM. 2000. The influence of fire on the germination of savanna tree seeds. In *Towards sustainable management based on scientific understanding of natural forests and woodlands. Proceedings: Natural forests and savanna woodlands symposium II*, Seydack AHW, Vermeulen WJ & Vermeulen C (Eds.), pp. 208-211. Department of Water Affairs and Forestry, Knysna, South Africa.

Sharon D. 1981. The distribution in space of local rainfall in the Namib desert. *Journal of Climatology* 1:69-75.

Shearing D. 1994. *Karoo. South African wild flower guide 6.* The Botanical Society of South Africa, Cape Town.

Shugart HH, Crow TR & Hett JM. 1973. Forest succession models: a rationale and methodology for modeling forest succession over large regions. *Forest Science* 19:203-212.

Siegel S & Castellan NJ. 1989. *Nonparametric statistics for the behavioural sciences.* McGraw-Hill Inc., New York.

Silander JA & Pacala SW. 1990. The application of plant population dynamic models to understanding plant competition. In *Perspectives on plant competition*, Grace JB & Tilman D (Eds.), pp. 67-91. Academic Press, San Diego.

Singh JS & Joshi MC. 1979. Ecology of the semi-arid regions of India with emphasis on landuse. In *Management of semi-arid ecosystems*, Walker BH (Ed.), pp. 243-275. Elsevier, Amsterdam.

Skarpe C. 1990a. Shrub layer dynamics under different herbivore densities in an arid savanna, Botswana. *Journal of Applied Ecology* 27:873-885.

Skarpe C. 1990b. Structure of the woody vegetation in disturbed and undisturbed arid savanna, Botswana. *Vegetatio* 87:11-18.

Skarpe C. 1991. Impact of grazing in savanna ecosystems. *Ambio* 20:351-356.

Skarpe C. 1992. Dynamics of savanna ecosystems. *Journal of Vegetation Science* 3:293-300.

Smit GN. 1999. Guide to the *Acacias of South Africa*. Briza Publications, Pretoria.

Smit GN. 2000. *Personal communication*, Calitzdorp, South Africa: Department of Grassland Science, University of the Free State, PO Box 339, Bloemfontein, 9300, South Africa.

Smit GN & Rethman NFG. 1992. Inter-related floristic changes associated with different long-term grazing treatments in Sourish mixed Bushveld. *Journal of the Grassland Society of Southern Africa* 9:76-81.

Smit GN & Rethman NFG. 2000. The influence of tree thinning on the establishment of herbaceous plants in a semi-arid savanna of southern Africa. *African Journal of Range and Forage Science* 16:9-18.

Smit GN & Swart JS. 1994. Influence of leguminous and non-leguminous woody plants on the herbeceous layer and soil under varying competition regimes in Mixed Bushveld. *African Journal of Range and Forage Science* 11:27-33.

Smith TM & Goodman PS. 1986. The effect of competition on the structure and dynamics of *Acacia* savannas in Southern Africa. *Journal of Ecology* 74:1031-1044.

Smith TM & Shackleton SE. 1988. The effects of shading on the establishment and growth of *Acacia tortilis* seedlings. *South African Journal of Botany* 54:375-379.

Snyman HA & Fouché HJ. 1991. Production and water-use efficiency of semi-arid grasslands of South Africa as affected by veld condition and rainfall. *Water SA* 17:263-268.

Soriano A & Sala O. 1983. Ecological strategies on a Patagonian arid steppe. *Vegetatio* 56:9-15.

Spinage CA & Guinness FM. 1971. Tree survival in the absence of elephants in the Akagira National Park, Rwanda. *Journal of Applied Ecology* 8:723-728.

Springuel I, Shaheen AS & Murphy KJ. 1995. Effects of grazing, water supply, and other environmental factors on natural regeneration of *Acacia raddiana* in an Egyptian desert wadi system. In *Rangelands in a sustainable biosphere. Proceedings of the Fifth International Rangeland Congress*, Vol. 1, pp. 529-530. Society for Range Management, Denver.

Strang RM. 1974. Some man-made changes in successional trends on the Rhodesian highveld. *Journal of Applied Ecology* 11:249-263.

Stuart-Hill GC & Tainton NM. 1988. Browse and herbage production in the Eastern Cape Thornveld in response to tree size and defoliation frequency. *Journal of the Grassland Society of Southern Africa* 5:42-47.

Stuart-Hill GC & Tainton NM. 1989. The competitive interaction between *Acacia karroo* and the herbaceous layer and how this is influenced by defoliation. *Journal of Applied Ecology* 26:285-298.

Stuart-Hill GC, Tainton NM, Aucamp AJ & Danckwerts JE. 1986. Infiltration and water use patterns in semi-arid South African savanna. In *Rangelands: a resource under siege. Proceedings of the Second International Rangeland Congress* (Adelaide 1985), pp. 465-466. Cambridge University Press, Cambridge.

Stuart-Hill GC, Tainton NM & Barnard HJ. 1987. The influence of an *Acacia karroo* tree on grass production in its vicinity. *Journal of the Grassland Society of Southern Africa* 4:83-88.

Swanson FJ & Sparks RE. 1990. Long-term ecological research and the invisible place. *BioScience* 40:502-508.

Tainton NM. 1984. A guide to the literature on research in the grassland biome of South Africa. *South African National Scientific Programmes Report No 96*. Foundation for Research Development, CSIR, Pretoria.

Teague WR. 1983. The expected response of *Acacia karroo* Hayne to moisture stress and defoliation. *Proceedings of the Grassland Society of Southern Africa* 18:147-150.

Teague WR. 1986. Response of *Acacia karoo* trees to intensity of defoliation at different phenophases in a South African savanna. In *Rangelands: a resource under siege. Proceedings of the Second International Rangeland Congress* (Adelaide 1985), pp. 466-467. Cambridge University Press, Cambridge.

Teague WR & Smit GN. 1992. Relations between woody and herbaceous components and the effects of bush-clearing in southern African savannas. *Journal of the Grassland Society of Southern Africa* 9:60-71.

Thalen DCP, Poorter H, Lotz LAP & Oosterveld P. 1987. Modelling the structural changes in vegetation under different grazing regimes. In *Disturbance in grasslands*, Van Andel J, Bakker JP & Snaydon RW (Eds.), pp. 167-183. Kluwer Academic Publishers Group, Dordrecht.

Thompson K. 1987. The resource ratio hypothesis and the meaning of competition. *Functional Ecology* 1:297-303.

Tiedemann AR & Klemmedson JO. 1977. Effect of mesquite trees on vegetation and soils in the desert grasslands. *Journal of Range Management* 30:361-367.

Tielbörger K & Kadmon R. 2000. Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology* 81:1544-1553.

Tilman D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. *Ecology* 58:338-348.

Tilman D. 1980. Resources: a graphical-mechanistic approach to competition and predation. *The American Naturalist* 116:362-393.

Tilman D. 1982. Resource competition and community structure. In *Monographs in population biology*, No. 17, May RM (Ed.). Princeton University Press, Princeton.

Tilman D. 1987a. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs* 57:189-214.

Tilman D. 1987b. On the meaning of competition and the mechanisms of competitive superiority. *Functional Ecology* 1:304-315.

Tilman D. 1988. Plant strategies and the dynamics and structure of plant communities. In *Monographs in population biology*, No. 26, May RM (Ed.). Princeton University Press, Princeton.

Tilman D & Pacala S. 1993. The maintenance of species richness in plant communities. In *Species diversity in ecological communities. Historical and geographical perspectives*, Ricklefs RE & Schluter D (Eds.), pp. 13-25. University of Chicago Press, Chicago.

Tinley KL. 1982. The influence of soil moisture balance on ecosystem patterns in South Africa. In *Ecology of tropical savannas*, Ecological studies Vol. 42, Huntley BJ & Walker BH (Eds.), pp. 175-192. Springer-Verlag, New York.

Tjepkema JD & Burris RH. 1976. Nitrogenase activity associated with some Wisconsin prairie grasses. *Plant and Soil* 45:81-94.

Tolsma DJ, Ernst WHO, Verwey RA & Vooijs R. 1987. Seasonal variation of nutrient concentrations in a semi-arid savanna ecosystem in Botswana. *Journal of Ecology* 75:755-770.

Trollope WSW. 1974. Role of fire in preventing bush encroachment in the Eastern Cape. *Proceedings of the Grassland Society of Southern Africa* 9:67-72.

Trollope WSW. 1980. Controlling bush encroachment with fire in the savanna areas of South Africa. *Proceedings of the Grassland Society of Southern Africa* 15:173-177.

Trollope WSW. 1982. Ecological effects of fire in South African savannas. In *Ecology of tropical savannas*, Ecological studies Vol. 42, Huntley BJ & Walker BH (Eds.), pp. 292-306. Springer-Verlag, New York.

Trollope WSW. 1987. Effect of season of burning on grass recovery in the false thornveld of the Eastern Cape. *Journal of the Grassland Society of Southern Africa* 4:74-77.

Trollope WSW. 2000. Effects and use of fire in southern African savannas. In *Towards sustainable management based on scientific understanding of natural forests and woodlands. Proceedings: Natural forests and savanna woodlands symposium II*, Seydack AHW, Vermeulen WJ & Vermeulen C (Eds.), pp. 142-144. Department of Water Affairs and Forestry, Knysna, South Africa.

Turner MG, Arthaud GJ, Engstrom RT, Hejl SJ, Liu J, Loeb S & McKelvey K. 1995. Usefulness of spatially explicit population models in land management. *Ecological Applications* 5:12-16.

Tybirk K, Schmidt LH & Hauser T. 1993. Notes on soil seed banks of African acacias. *African Journal of Ecology* 32:327-330.

Van Andel J & Van den Bergh JP. 1987. Disturbance of grasslands. Outline of the theme. In *Disturbance in grasslands*, Van Andel J, Bakker JP & Snaydon RW (Eds.), pp. 3-13. Kluwer Academic Publishers Group, Dordrecht.

Van Auken OW & Bush JK. 1989. *Prosopis glandulosa* growth: influence of nutrients and simulated grazing of *Bouteloua curtipendula*. *Ecology* 70:512-516.

Van Auken OW, Gese EM & Connors K. 1985. Fertilization response of early and late successional species: *Acacia smallii* and *Celtis laevigata*. *Botanical Gazette* 146:564-569.

Vance RR. 1984. Interference competition and the coexistence of two competitiors on a sigle limiting resource. *Ecology* 65:1349-1357.

Van der Schijff HP. 1964. 'n Hervaluasie van die probleem van bosindringing in Suid-Afrika. *Tydskrif van Natuurwetenskappe* 4:67-80.

Van Niekerk JP & Kotze T. 1977. Chemical control of bush encroachment by means of aerial spraying. In *Proceedings of the Second National Weeds Conference of South Africa*, pp. 165-184. A.A. Balkema, Cape Town.

Van Oudtshoorn F. 1999. *Guide to grasses of Southern Africa*. Briza, Cape Town.

Van Riet and Louw Landscape Architects & Metaplan. 1999. *Kimberley Triangle community resource project*. Pretoria.

Van Rooyen N, Theron GK & Bredenkamp GJ. 1991. Long term vegetation dynamics in the semi-arid Kalahari. *Koedoe* 34:91-92.

Van Vegten JA. 1983. Thornbush invasion in a savanna ecosystem in eastern Botswana. *Vegetatio* 56:3-7.

Van Wilgen BW & Scholes RJ. 1997. The vegetation and fire regimes of southern hemisphere Africa. In *Fire in southern African savannas. Eoclogical and atmospheric perspectives*, Van Wilgen BW, Andreae MO, Goldammer JG & Lindesay JA (eds.), pp. 27-46. Witwatersrand University Press, Johannesburg.

Vitousek P. 1982. Nutrient cycling and nutrient use efficiency. *The American Naturalist* 119:553-572.

Vitousek PM, D'Antonio CM, Loope LL & Westbrooks R. 1996. Biological invasions as global environmental change. *American Scientist* 84:468-479.

Vogel CH. 1988a. Climatic change in the Cape Colony, 1820-1900. *South African Journal of Science* 84:11.

Vogel CH. 1988b. 160 years of rainfall of the Cape – has there been a change? *South African Journal of Science* 84:724-726.

Walker BH & Knoop WT. 1987. The response of the herbaceous layer in a dystrophic *Burkea africana* savanna to increased levels of nitrogen, phosphate and potassium. *Journal of the Grassland Society of Southern Africa* 4:31-34.

Walker BH & Noy-Meir I. 1982. Aspects of the stability and resilience of savanna ecosystems. In *Ecology of tropical savannas*, Ecological studies Vol. 42, Huntley BJ & Walker BH (Eds.), pp. 556-590. Springer-Verlag, New York.

Walker BH, Ludwig D, Holling CS & Peterman RM. 1981. Stability of semi-arid savanna grazing systems. *Journal of Ecology* 69:473-498.

Walker J & Gillison AN. 1982. Australian savannas. In *Ecology of tropical savannas*, Huntley BJ & Walker BH (Eds.), pp. 5-24. Springer-Verlag, New York.

Walter H. 1971. *Ecology of tropical and subtropical vegetation*. Oliver & Boyd, Edinburgh.

Wand SJE, Midgley GF & Musil CF. 1996. Physiological and growth responses of two African species, *Acacia karroo* and *Themeda triandra*, to combined increases in CO_2 and UV-B radiation. *Physiologia Plantarum* 98:882-890.

Ward D. 2000. *Rangeland vegetation overgrazing and recovery – Namibia*. Final Report to US Agency for International Development, Tel Aviv, Israel.

Ward D. 2001, in press. The effects of grazing on plant biodiversity in arid ecosystems. In *Dryland biodiversity*, Waide R, Gosz J & Shachak M (Eds.). Oxford University Press, Oxford.

Ward D & Seely MK. 1996. Competition and habitat selection in Namib desert tenebrionid beetles. *Evolutionary Ecology* 10:341-359.

Watt AS. 1947. Pattern and process in the plant community. *Journal of Ecology* 35:1-22.

Weltzin JF, Archer S & Heitschmidt RK. 1997. Small-mammal regulation of vegetation structure in a temperate savanna. *Ecology* 78:751-763.

Werner PA, Walker BH & Stott PA. 1990. Introduction. *Journal of Biogeography* 17:343-344.

Westoby M, Walker B & Noy-Meir I. 1989. Range management on the basis of a model which does not seek to establish equilibrium. *Journal of Arid Environments* 17:235-239.

Wickens GE. 1969. A study of *Acacia albida* Del. (Mimosoideae). *Kew Bulletin* 23:181-202.

Wiegand K, Jeltsch F & Ward D. 1999. Analysis of the population dynamics of *Acacia* trees in the Negev desert, Israel with a spatially-explicit computer simlulation model. *Ecological Modelling* 117:203-224.

Wiegand K, Ward D, Thulke H & Jeltsch F. 2000a. From snapshot information to long-term population dynamics of Acacias by a simulation model. *Plant Ecology* 150:97-114.

Wiegand K, Saltz D & Ward D. 2000b, submitted. A unifying patch dynamics approach to savanna dynamics and bush encroachment / Multi-scale patterns. *Ecological Applications.*

Wiegand K, Saltz D & Ward D. 2000c, in review. Bush encroachment dynamics in a single soil layer arid environment. *Journal of Ecology.*

Wiegand K, Jeltsch F & Ward D. 2000d. Do spatial effects play a role in the spatial distribution of desert-dwelling *Acacia raddiana*? *Journal of Vegetation Science* 11:473-484.

Wiegand K, Schmidt H, Jeltsch F & Ward D. 2000e. Linking a spatially-explicit model of Acacias to GIS and remotely-sensed data. *Folia Geobotanica* 35:211-230.

Wiens JA. 1977. On competition and variable environments. *American Scientist* 65:590-597.

Wiens JA. 1984. On understanding a non-equilibrium world: myth and reality in community patterns and processes. In *Ecological communities. Conceptual issues and the evidence*, Strong DR, Simberloff D, Abele LG & Thistle AB (Eds.), pp. 439-457. Princeton University Press, Princeton.

Wilson JB. 1988. Shoot competition and root competition. *Journal of Applied Ecology* 25:279-296.

Wilson SC & Keddy PA. 1986. Measuring diffuse competition along an environmental gradient: results from a shoreline plant community. *The American Naturalist* 127:862-869.

Wilson TB & Witkowski ETF. 1998. Water requirements for germination and early seedling establishment in four African savanna woody plant species. *Journal of Arid Environments* 38:541-550.