# EFFECTS OF HERBIVORES, FIRE AND HARVESTING ON THE POPULATION DYNAMICS OF *ACACIA DREPANOLOBIUM* SJOESTEDT IN LAIKIPIA, KENYA

By

**BELL DEDAN OKELLO**

**Submitted in fulfilment of the academic requirements**

**For the degree of**

**Doctor of Philosophy**

**in the**

**Discipline of Grassland Science,**

**School of Biological and Conservation Sciences**

**University of KwaZulu-Natal**

**Pietermaritzburg**

**2007**

# PREFACE

The experimental work described in this thesis was carried out in the Discipline of Grassland Science, School of Biological and Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg, from June 1996 to December 2000, under the supervision of, Professor Timothy G. O'Connor, Professor Truman P. Young and Professor Kevin Kirkman.

DECLARATION

I declare that these studies represent my original work and have not otherwise been submitted in any form for any degree to any University. Where use has been made of the work of others it is duly acknowledged in the text.

SIGNED Bell D. Okello

Date:

SIGNED Prof. Timothy G. O’Connor: Supervisor

Date:

SIGNED Prof. Kevin Kirkman: Co-supervisor

Date:

SIGNED Prof. Truman P. Young: Co-supervisor

Date:

# ACKNOWLEDGEMENTS

Many people and institutions made immense contributions in one way or another towards the research and write up of this thesis, and I sincerely thank them all. Mpala Citi-Bank fellowship through the late George Small, Nick Georgiadis and Truman Young, The International Foundation for Science (IFS) grant, Leslie Scott and, Truman Young's grants through the National Geographic, The National Science Foundation, Smithsonian Institute, Luis Calder Foundation at Fordham University, and the University of California at Davis gave fellowships and research grants that funded this study. The late George Small, Nick Georgiadis and John Smith come for special mention because they offered the facilities to conduct the research at Mpala; they also provided a lot of logistic assistance during the study.

Special gratitude goes to Prof. Tim O'Connor, Prof. Truman Young and Prof. Kevin Kirkman, for their guidance, patience and sacrifice while supervising this study. Dr. T. J. Njoka was of great inspiration to me before and during the study.

Many thanks to all the visiting scientists, my colleagues and the staff at Mpala Research Centre; colleagues C. Morris, G. Naiken, M Goddard, D. Kotze and all the graduate students of the Grassland Science Discipline at the University of KwaZulu-Natal, Pietermaritzburg. Sincere thanks to the staff at Mpala especially Fredrick Erii, Steve Ekuang'a, Francis Ewaton, and John Lemboi who were able field assistants at different times. Debbie Nordstrom, Karma Wolf, and Kerrie Houghton from Canada voluntarily assisted with data collection for three rainy months. My family, especially wife Grace encouraged and supported me to finish and submit this thesis after many months on the shelves.

I deeply appreciate the assistance of the technical staff at the Departments of Range Management, Soil Science and Animal Production, University of Nairobi for assisting with the analysis of various plant and soil samples. The Entomology Department at the National Museums of Kenya assisted with identification of ants, beetles and wasps.

Last but not least, I thank God, for giving me guidance, strength and good health that enabled me to conduct this study.

# DEDICATION

I dedicate this thesis to my late parents, Hoseah Odack Ayub and Theresa Aketch Odack for having sent me to school and inculcated in me, the value of hard work and education.

# TABLE OF CONTENTS

## LIST OF TABLES

## LIST OF FIGURES

# ABSTRACT

Effects of herbivory, fire, and tree harvesting on *Acacia drepanolobium* were studied using plant population dynamics as the philosophical basis of research. Specifically, growth rates, chrono-sequence of re-growth, biomass and charcoal yield, herbivory, flowering, seed production, germination, mortality and the ants of *Acacia drepanolobium* were studied in the black cotton ecosystem of Mpala Research Centre, Laikipia, Kenya, between September 1995 and December 2000.

*Acacia drepanolobium* was the most abundant tree or shrub with densities ranging from 80% to 98% of all the overstorey species, but it was the least browsed of all the trees and shrubs in the black cotton ecosystem, ranging from a mean of 7.2% to 9% of the individuals browsed. The tree is inhabited by four *Acacia* ant species, *Crematogaster mimosae*, *Crematogaster sjoestedti, Crematogaster nigriceps,* and *Tetraponera penzigi,* which are believed to be obligate, and which probably play a role in the low browsing rates observed.

Six herbivore treatments replicated three times (no herbivores - O; only cattle - C, all herbivores allowed - MWC {control}, mega-herbivores {elephants and giraffe} and wildlife {W} – MW only, wildlife – W - only {all wildlife except mega-herbivores} and wildlife and cattle only - WC) was the main experimental design used in understanding the dynamics of the tree species under influence of different herbivores.

Mean annual height growth of *A. drepanolobium* trees was 24.9 cm $yr^{-1}$, while the mean Relative Growth Rates ranged from $14.6 \times 10^{-3}$ cm $cm^{-1}$ $yr^{-1}$ to $18.7 \times 10^{-3}$ cm $cm^{-1}$ $yr^{-1.}$ Growth rates were different among the herbivore treatments and between seasons. Shoots of the tree grew by a mean range of 6.8 cm to 9.1 cm, were similar among the treatments but differed among the seasons.

Canopy volume increased over time although it fluctuated with seasons, suggesting an increase in bushiness of *A. drepanolobium* in the ecosystem. Trees occupied by different ant species showed differences in shoot density (number of new shoots per twig), being greater in *Crematogaster nigriceps* occupied trees compared with the other ant species. Swollen thorn (gall) density per unit of twig length was greatest in treatments with mega-herbivores; these galls were significantly larger on trees occupied by the ant *Crematogaster nigriceps.*

Treatments with herbivores were more spinescent than the total exclusion treatment. Spine lengths ranged from 0.8 to 2.4 cm, and recorded a progressive reduction of up to 36.7% in treatments without browsers suggesting a relaxation of induced defence in *A. drepanolobium*.

Flowering in *A. drepanolobium* was low and staggered over the study period ranging from 0.8% to 2.0% of the trees with no differences among the treatments suggesting that the level of herbivory was not sufficient to influence reproduction of the tree in the experimental site. Consequently, seedling recruitment was very low within the experimental site. However, a nearby site recorded flowering of between 22.7% and 93.5%. Mean pod production, mean number of seeds per tree and mean weight of pods and seeds had a positive linear relationship with tree density ($R^2$=0.77, 0.81 and 0.81 respectively). Trees occupied by *Crematogaster mimosae* were the most likely to flower (68%) compared with *C. nigriceps* (5.8%), again suggesting that ants had an effect on the tree's reproduction.

Mortality of *A. drepanolobium* trees averaged 0.9% to 4.2% over the study period, being significantly greater in treatments with mega-herbivores. Seedling survival ranged from 42% to 75%, being greatest in the cattle only treatment. Between 30% and 100% (mean 67.2%), of *A. drepanolobium* seeds were attacked by a bruchid beetle (*Bruchus* sp.). Seeds attacked by bruchid beetles had significantly lower germination rates. Similarly, seeds passed through a fire also recoded significantly low germination rates compared with normal seeds. Fire (3.4%) and bruchid beetles (20.7%) germination compared with (control) undamaged seeds (84%) play an important role in the population dynamics of *A. drepanolobium*. Fewer *A. drepanolobium* seeds (33%) were recovered from the surface compared with buried (72%) seeds after a fire, indicating seed loss from the effect of fire and predation.

In the burn experiment, fire top-killed 16% of *A. drepanolobium* trees but no tree or seedling was killed. On the other hand, fire significantly reduced the density of non-*A. drepanolobium* trees by between 50% and 100%, with none of them showing signs of coppicing after the fire unlike top-killed *A. drepanolobium* trees.

Woody biomass from *A. drepanolobium* was strongly related to stem diameter ($Y = 3.77x + 1.17$, R2 = 0.96, $P < 0.001$). Mean charcoal production from earthen kilns was 2.83 Mg $ha^{-1}$. Height and stem diameter in coppicing stands increased at a mean rate of 28.6 cm $yr^{-1}$ and 0.7 cm $yr^{-1}$ respectively. Biomass in coppicing stands accumulated at a mean rate of

1.3 Mg $ha^{-1}$ $yr^{-1}$ in a 14-year period, yielding dry biomass of 18.26 Mg $ha^{-1}$ useable wood that can produce a minimum of 3.0 Mg $ha^{-1}$ of charcoal.

This study shows that *Acacia drepanolobium* populations are affected by several factors including herbivory, fire and ants. The population dynamics of this tree shows that it can be harvested for sustainable charcoal yield over a 14-year cycle.

# 1 CHAPTER ONE: INTRODUCTION

## 1.1 BACKGROUND INFORMATION

### 1.1.1 Importance of savanna ecosystems

Over 80% of Kenya's land surface is arid and semi-arid rangeland, most of which is *Acacia* savanna (Pratt & Gwynne 1977; Herlocker 1999). These lands directly support at least 25% (Ayuko 1978) of Kenya's 28.9 million people (Central Bureau of Statistics 2005), and are home to a large biomass of indigenous and domestic herbivores as well as a diverse flora (Heady & Heady 1982). According to the 5th National Development Plan of Kenya (1986), and the Economic Recovery Strategy (ERS 2004) paper, arid and semi-arid lands (ASAL) are becoming increasingly important in absorbing and meeting the needs of the ever-increasing human population.

Savanna ecosystems are important in maintaining the large biomass of domesticated and a diverse array of indigenous herbivores (Sinclair & Norton-Griffiths 1979), and are of especial importance to ranching and conservation activities (Myers 1972; Grootenhuis 1990). Specifically for Kenya, the functioning and well-being of savannas is crucial for the survival of the tourism industry, an important earner of foreign exchange (Western & Henry 1979; Western 1989, Economic Survey 2005). The savannas are also important in provision of goods and services to mankind e.g. food, fuelwood, building materials and medicine (FAO 1996).

Despite their importance, many savanna ecosystems are facing problems that threaten their productivity. One major problem is bush encroachment (Van Vegten 1983), and woody invasion of grasslands, or increase in woody density within savannas, is now recognised as a vegetation dynamic of increasing global significance (Kriticos *et al*. 1999).

Bush encroachment in many African savannas has been ascribed to overgrazing, especially by livestock (Walker *et al*. 1981; Milton & Dean 1995; Herlocker 1996), e.g. *Acacia karroo* in Eastern Cape of South Africa (O'Connor & Crow 1999), *A. mellifera* (Vahl) Benth. *A. etbaica* Sweinf. in Mukogodo of Laikipia, Kenya (Mwihuri 1998) and *A. reficiens* in Samburu (which neighbours Laikipia), although Okello (1996) reported bush encroachment on some commercial ranches within Laikipia, Kenya, where herbivore numbers (particularly livestock) have been extremely low for more than 30 years.

Bush encroachment is a problem in rangelands because trees and shrubs may obstruct access to forage for certain herbivores, compete with the herb layer for light, water and soil nutrients, reduce herbaceous production and undermine other uses of land (Coppock 1990). Therefore, bush encroachment compromises the quality and quantity of products and services from rangelands.

In order to conserve valuable forage in rangelands, there is need to prevent the ingress of invasive woody plants of low forage value in accordance with existing production goals before they decrease the valuable ones (Brown *et al*. 1998). A case in point is *Acacia reficiens*, which has now become a bush problem in the northern rangelands of Samburu (SNV 2002). *Prosopis juliflora,* which was introduced to alleviate rangeland degradation in northern Kenya has now colonised thousands of hectares of rangelands in Kenya (NEMA 2005) and become a big bush problem. To mitigate the effects of bush encroachment, the dynamics of invasive species and factors that drive it should be understood (Kriticos *et al*. 1999). It is also essential that the potential of 'problem' woody species be explored in order to develop appropriate and sustainable management options to harness them.

A second problem in savanna ecosystems is a conflict in demand for land use between livestock production and wildlife conservation (Western & Henry 1979; Western & Gichohi 1993; Herlocker 1999). Livestock and wildlife share much of their respective ranges in most East African savannas (Njoka 1990). As the profitability of livestock production becomes marginal and wildlife values increase, there is a need to understand the interactions between livestock and indigenous wild mammalian herbivores and their habitats. Though the relationship between livestock and wildlife are often viewed negatively (Prins 1992), many wildlife species are not incompatible with moderate livestock production and their relationship may even be beneficial (Hopcraft 1990).

Semi-arid and arid ecosystems are facing rapidly increasing pressure for intensive cattle production, game ranching, arid land crop farming and other uses including mining (Gichohi *et al*. 1996). These pressures can result in local, regional as well as global environmental problems e.g. soil erosion (Liniger 1992), threats to biodiversity (Steenkamp & Chown 1996; Young 1996; Higgins *et al.* 1999) and even desertification (Dregne 1986; FAO 1996).

### 1.1.2 Mechanisms of bush encroachment

The rates of encroachment by any species depends on *inter alia*, its seed production, seed longevity, dispersal, germination rates, palatability and consumption by herbivores (Kriticos *et al*. 1999), indicating that rates of woody invasion may be species specific. Other factors known to influence the rate and pattern of bush encroachment include rainfall variability (Scanlan & Archer 1991), fire (Pellew 1983; Oba 1990), browsing (Lock 1993) and grazing (Pratt & Knight 1971).

Seedling recruitment is the critical phase by which bush encroachment is enhanced (Brown *et al*. 1998). Seedling recruitment may depend on the availability of seeds (hence seed banks), their dispersal (therefore dispersal agents), and on conducive environmental conditions including soils, climate, and fire for germination and establishment (Brown & Carter 1998). The process of woody invasion of grasslands may be triggered by a number of factors, e.g. episodic events that enhance germination of seedlings, decrease in herbivore pressure resulting in high rates of seedling survival, or even fires that trigger germination (Coe & Coe 1987). The hand of man is often visible in many of these events, for man controls to a large extent fire, herbivore numbers and their movements in most rangelands (Christensen 1997). Hence, the type of management employed may determine the rate and extent of bush encroachment (Rohner & Ward 1999). The patterns of encroachment are likely to mirror the rates and processes of invasion.

### 1.1.3 Traditional range management tools

In many rangelands the world over, pastoralists and range managers maintained a healthy and profitable balance between the herb and woody layers through grazing (using different mixes of animals), and burning (Coppock 1990). However, the likelihood of effective fire occurring has declined in many rangelands because of a decrease in the fuel load and a reduction in the area of land available for burning due to demand from other uses of land arising from growth in human population. In some ranges, the use of fire is considered environmentally unfriendly. Mechanical removal (Back 1998), which is usually labour intensive, expensive, and may affect the environment especially if heavy machinery is used; chemical control (Outrum 1970; Pratt & Gwynne 1977; Back 1998), which may be expensive and environmentally unfriendly; biological control (Kriticos *et al.* 1999), and the maintenance of a mix of grazers and browsers (Coppock 1990), are other methods used in managing bush encroachment with varying degrees of success.

### 1.1.4 Herbivory and fire in savannas

Herbivory and its effects has been a subject of research in savanna ecosystems for many years (Sinclair & Norton-Griffiths 1979; Sinclair & Arcese 1995). Herbivores (e.g. elephant and giraffe) can modify vegetation, especially the woody component (Lock 1993; Dublin 1995; Leuthold 1996), while a high density of grazers can lead to bush encroachment (Swift *et al.* 1996). Despite all these studies, our understanding of these ecosystems is still incomplete, and we are still far from using these lands sustainably (Gichohi *et al*. 1996; Swift *et al.* 1996).

Fire is an important range management tool, and probably the most potent factor that shaped savanna ecosystems in the past (Oba 1990). However, the frequency of fire use has decreased over the years and this is manifested in the present vegetation structure dominated by trees/shrubs and grasses of low palatability (Mwihuri 1998). Contemporary conditions in savannas of decreased land size, erratic rainfall, higher animal numbers, and increase in bush encroachment, call for a scientific re-evaluation of how these lands are managed and use of the most appropriate tools/approaches.

Because of the problems being experienced in arid and semi-arid areas, management of these lands worldwide is undergoing re-evaluation, with emphasis on management programmes that are sustainable and compatible with the native biodiversity. A solid understanding of the ecology and dynamics of these ecosystems is central to their long-term development, management and conservation (Bourliere 1983; Tothill & Mott 1985). It is recognised that a detailed understanding of an entire savanna ecosystem with the complex suite of issues and factors, is nearly impossible. However, individual populations can be examined in detail to unravel the underlying dynamics. Such examination should of necessity be based on the current land use systems, future projections based on emerging scenarios, and should incorporate inputs from rangeland users, planners and managers.

## 1.2 THE PROBLEM

In the Laikipia District of north central Kenya, at least 75% of the land surface is classified as rangeland (Taiti 1992). These rangelands are extensively used for livestock ranching or traditional pastoralism and are also home to the largest biomass of wildlife outside national parks and game reserves in the country (Grootenhuis *et al*. 1990). At least 35% of Laikipia District is covered by black cotton soils derived from volcanic rocks (Ahn & Geiger 1987; Taiti 1992) that are poorly drained. *Acacia drepanolobium* is the dominant overstorey species in these rangelands with black cotton soils. Some attributes of *Acacia drepanolobium* in this ecosystem are:

1) Other *Acacia* species are either absent or occur in insignificant numbers where it dominates, especially in black cotton soils.

2) *Acacia drepanolobium* occurs largely in mono-specific stands in which there are very few other tree or shrub species.

3) Individual stands of *A. drepanolobium* are often characterised by very different maximum tree heights.

4) At least four *Acacia*-ant species live within its swollen thorns but their roles are not well understood.

5) It coppices readily when harvested or burnt.

6) It can serve as an excellent source of wood for sustainable charcoal production.

Most ranchers in *Acacia drepanolobium* areas alleged, during informal discussions, that this species has increased its density over the last 30 to 40 years. Some ranchers have labelled it a problem species because; a) *Acacia drepanolobium* coppices readily in response to top kill by fire or harvesting; b) it is of low forage value since it is heavily defended against herbivory by spines and ants; c) it is increasing in density; d) *Acacia drepanolobium* has not been successfully controlled by chemical and physical means; and e) *Acacia drepanolobium* has suppressed grass production in some areas. The ranchers expressed their desire to know how to effectively manage areas with *A. drepanolobium* at low cost and on a sustainable basis without totally eliminating it. In areas where *A. drepanolobium* was not a ‘problem’, ranchers expressed a need to understand how the large biomass of domestic animals and indigenous wildlife affects the tree.

Most ranches in Laikipia stopped using fire as a range management tool in the early 1970s, and *A. drepanolobium* has also re-colonised areas in which Tordon® (a mixture of Pichlorum and 2,4-D) was applied to reduce or eliminate it (Outrum 1970). Though there are still occasional out-breaks of wildfires, the efficacy of fire as a tool in range management in these ecosystems is unclear.

Large areas of *Acacia drepanolobium* on many ranches are cleared for roads, paths, and to create grass leys, and most of the wood is used in traditional earthen kilns for charcoal production or firewood (pers. observation), but neither the rates of *A. drepanolobium* re-growth, nor the production of woody biomass and charcoal are known.

## 1.3 PHILOSOPHY OF THESIS

Plants occupy space to the maximum possible extent and so plant communities usually appear full. However, plant populations are dynamic, driven by several internal and external factors. Several approaches have evolved to study how plant populations change and the forces that drive the changes including population dynamics (Silvertown & Doust 1993), community dynamics (Sinclair & Norton-Griffiths 1979; Sinclair & Arcese 1995), landscape ecology (Ostfeld *et al.* 1997; Rogers 1997), probing resource availability theories (Bryant *et al*. 1989), and patch dynamics (Pickett & White 1985). These approaches are not mutually exclusive. The philosophy of population dynamics has the advantage of distinguishing causes and effects at different stages of a plant's life, and thus identifies more succinctly where management can intervene to direct desired changes (Kriticos *et al*. 1999).

Because changes that occur among plant populations may have consequences for the overall functioning of the ecosystem, forces driving these changes must be well understood for the sustainable management of these ecosystems to be realised. The rates of inputs and outputs from a plant community as well as the factors that influence and drive these rates are critical in determining changes in plant populations. These factors include flowering and seed production, germination and establishment, herbivory, growth of individual plants and whole populations, and survival rates of seeds, seedlings and mature plants.

Environmental factors (e.g. rainfall) play a crucial role in these dynamics because the phenology of most species responds to the amount, duration, and season of rainfall (Pratt & Gwynne 1977). Herbivory may also influence certain stages in a plant's life cycle

(Sinclair & Arcese 1995). In areas where fire is still a management tool, it may determine whether some seeds germinate or not, whether seedlings survive or die, and in some cases may kill mature trees and shrubs, (e.g. *A. tortilis* in Turkana (Oba 1990)).

To elucidate the different factors that affect the population dynamics, experimental manipulations at field level were used. These manipulations offer empirical evidence for the observed phenomena. However, studies that use experimental manipulations at a system level are not common in African savannas (Young *et al*. 1998), and the results of this study are the first for East African savannas.

The philosophy behind this thesis is that a study of population dynamics will provide critical insights for understanding the influence of disturbances such as herbivory, fire and harvesting on the dynamics of *Acacia drepanolobium*, from which practical options for management may be formulated. The need to make available robust information that will assist ranchers, managers, planners, conservationists and scientists to improve the profitability and effectiveness of their long-term range management was the motivation behind this study, and the influence of herbivores, fire and harvesting on the population dynamics of *A. drepanolobium* were selected as the focus of study.

## 1.4 OVERALL OBJECTIVE AND QUESTIONS ADDRESSED IN THE STUDY

The overall objective of this study was to investigate the effects of herbivory by cattle and large indigenous game and fire on the population dynamics of *Acacia drepanolobium*, and to evaluate its suitability for sustainable harvesting of wood for charcoal production.

The main issues addressed in the study were the following:

1. The effects of herbivory by large mammals on populations of *A. drepanolobium* in the black cotton ecosystem;
2. Seed ecology of *A. drepanolobium;*
3. The effects of fire on the demography of *A. drepanolobium* and herb layer species composition and cover for managing *A. drepanolobium* dominated woodlands;
4. Use of stands of *A. drepanolobium* for profitable and sustainable charcoal harvest; and
5. Role of *Acacia* ants in the population dynamics of *A. drepanolobium*.

### 1.4.1 Structure of thesis

This thesis is made up of nine chapters; chapter one provides a detailed introduction that includes the background, rationale and the broad objectives of the research. Chapter two examines current literature on the subject of *Acacia drepanolobium* and related species with reference to the theme of the study. The chapter culminates in a detailed description of the study objectives that correspond to the overall objective and the main issues addressed by the study. In chapter three, the species of study and the study area are described, and the overall structure of the experiment is outlined.

Chapters four to eight present the key findings and discussions on the major questions the study addressed. Each of these chapters has a short introduction, a detailed methods section including data analysis, a results section and the discussion arising from the presentation. Chapter four explores the influence of herbivory on the population dynamics of *A. drepanolobium,* specifically rates of growth and mortality, and utilization by herbivores. The seed ecology of *A. drepanolobium,* including how the seeds are affected by fire and bruchid beetles, is examined in chapter five. Chapter six discusses the effects of fire on the population dynamics of *A. drepanolobium*. The biomass yields, chrono-sequence of re-growth and potential for charcoal production from *A. drepanolobium* are presented in chapter seven. Chapter eight explores the relationships between *A. drepanolobium* and its *Acacia*-ants. A summary of the entire study is presented in chapter nine. Conclusions, recommendations, options for management implementation and focus for future research are also presented. At the end of the thesis, abstracts of scientific papers arising from the study, which have been submitted, accepted or published are included as part of the Appendix.

Nomenclature of plants in this thesis follows that of Bogdan (1958), Ross (1979), Coe & Beentje (1991), Agnew & Agnew (1994) and Beentje (1994). Nomenclature of animals follows Dorst & Dandelot (1972), Estes (1991), and Kingdon (1997).

# 2 CHAPTER TWO: LITERATURE REVIEW

## 2.1 BACKGROUND TO EAST AFRICAN SAVANNAS

A salient feature of arid and semi-arid lands (ASAL) in East Africa is the expansive savanna ecosystem. Savannas have been described as lands within an almost closed or continuous herbaceous stratum interspersed with a discontinuous ligneous or woody component of varying density (Belsky 1984; Menault *et al.* 1985; Kinyamario *et al*. 1995). Both the ligneous and herb layers in savanna ecosystems are important in maintaining the large biomass of domestic herbivores and a diverse array of wildlife, and especially important to pastoralism, ranching and wildlife conservation (Myers 1972; Western & Gichohi 1993).

Although both the herb and woody layers of savannas have received considerable scientific attention in the last five decades (Norton-Griffiths 1979; Sinclair & Norton-Griffiths 1979; O'Connor 1985; Sinclair & Arcese 1995; McClanahan & Young 1996), interest in the browse component is only starting to receive its due attention (e.g. reviews by Walker 1976; Le Houe`rou 1980; O'Connor 1996; Smit *et al.* 1996). The knowledge of the browse component of African savannas is, at best, still fragmentary (O'Connor 1996).

### 2.1.1 Factors influencing savanna structure and function

The distribution, structure and functioning of savanna vegetation, especially of the browse component, is determined by many factors acting singly or in concert (Walker *et al.* 1981; Belsky 1984; Ruess & Halter 1990; Skarpe 1992). These factors include the physical environment, e.g. soils, climate, especially rainfall, aspect and altitude (Pratt & Gwynne 1977; Heady 1978; Belsky 1995; Gichohi *et al*. 1996; O'Connor 1999), the biotic environment, especially herbivores (Norton-Griffiths 1979; Pellew 1983; McNaughton & Georgiadis 1986; Ben-Shakar 1991), fire (Edroma 1984; O'Connor 1985; Edroma & Wein 1986; Dublin 1995; Roques *et al* 2001) and human use (Tietema *et al*. 1991). Human use is increasingly becoming a major determinant of savanna structure and function (Western & Gichohi 1993).

### 2.1.2 Uses of *Acacia* species in savannas

In many African savannas, *Acacia* species are the most important group of browse species (Ross 1979; Fagg & Stewart 1994). *Acacia* species provide forage to herbivores especially during the dry seasons (Haro & Oba 1993; Bentje 1994; Fagg & Stewart 1994; Okello

1996), are a source of shelter (Pratt & Gwynne 1977) and building materials (Deshmukh 1992; Wyant & Reid 1992; Haro & Oba 1993). They are important in nitrogen fixation (Kinyua 1996), bind soils with their root systems and thereby reduce soil erosion (Kironchi 1992; Liniger 1992; Mutunga 1995), and some are crucial in the survival of certain herb layer species, e.g. *Panicum maximum* Jacq. (Maranga *et al*. 1983; Kinyamario *et al*. 1995). *Acacia* species are also an important source for human food including honey (Taiti 1992).

African *Acacia* species thus play a key role in maintaining the rich biodiversity of these savannas. However, there is little knowledge on the population dynamics of most *Acacia* species (Eshete & Stahl 1999; Wiegand *et al*. 1999), and especially how they respond to disturbances from herbivores, fire and human use (Young *et al*. 1997).

## 2.2 BUSH ENCROACHMENT: CAUSES, PATTERNS AND CONCEPTS

A common observation in many savanna ecosystems the world over, is bush encroachment (Lock 1993; Leuthold 1996; Back 1998; Higgins *et al*. 1999). Bush encroachment or woody invasion of grasslands is one of the main problems facing scientists and managers in arid and semi-arid savannas, and has assumed great global significance in recent years (Kriticos *et al.* 1999; O'Connor & Crow 1999).

Bush encroachment is a problem because the trees and shrubs may: 1) obstruct access to forage for certain herbivores (Coppock 1990); 2) compete with the herb layer for light, water and other nutrients thus lowering primary production (Sabiiti & Wein 1988) and therefore, livestock production (Mbuvi & Croze 1986); and, 3) may undermine other uses of land, and act as reservoirs for disease vectors e.g. tsetse flies (Lock 1993).

Many savanna ecosystems face bush encroachment problems, examples are: A*. karroo* in eastern Cape, South Africa (O'Connor & Crow 1999), *A. tortilis* in the Tsavo East National Park, Kenya (Leuthold 1996), *A. mellifera* in Laikipia, Kenya (Okello 1996), *A. drepanolobium* in the southern Ethiopian rangelands (Coppock 1990) and *A. sieberiana* in Queen Elizabeth National Park, Uganda (Lock 1993), and *Acacia reficiens* (SNV 2002). Bush encroachment is often compounded by alien invasive species, e.g. *Acacia nilotica* in northern Australia (Kriticos *et al.* 1999). Bush encroachment in the savannas is not limited to the genus *Acacia* only. *Prosopis juliflora* is an invasive weed in Kenya (NEMA 2005) and India (ICRA 1999), while *Dichrostachys cinerea* is a problem in Swaziland (Roques *et al.* 2001).

### 2.2.1 The process and causes of bush encroachment in savannas

The mainstream hypothesis on the cause of bush encroachment in these savannas is that overgrazing principally by livestock is the cause (Walker *et al*. 1981; Herlocker 1996). Withdrawal of fire has also been widely cited as a major reason (Dublin 1995). However, withdrawal of fire may result from overgrazing due to inadequate fuel to burn the range (Pellew 1983). The theory that overgrazing results in bush encroachment has been questioned (Brown *et al*. 1998), and it is possible that a combination of overgrazing and lack of fires, in combination with the type of management employed (due to inadequate understanding of savanna dynamics), may be the cause. However, it is recognised that bush encroachment does take place even in the absence of livestock (Okello 1996).

Bush encroachment typically begins with seedling recruitment, which is believed to be the critical phase (Brown *et al.* 1998) in woody invasion of savannas. This indicates that there is a healthy seed bank or presence of enough quantities of seed, and effective seed dispersal agents (Cavanagh 1980) including herbivores. In addition, environmental conditions for germination must also be appropriate. Episodic events may also play a role in triggering bush encroachment in savannas (Young & Lindsay 1988).

Before the advent of commercial ranching and in range areas still under traditional pastoralism, pastoralists maintained a balance between the woody and herbaceous layers by means of fires and keeping a mix of herds that maximised utilization of both vegetation layers (Coppock 1990), but this is no longer the case because of decreased land size in relation to the stock numbers held, so that little or no land is spared for burning.

### 2.2.2 Methods of controlling bush encroachment in savannas

Contemporary techniques used in many rangelands for mitigating the effects of bush encroachment include, *inter alia,* mechanical clearing (Back 1998), but this may be expensive and also destructive to the environment especially when heavy machinery is employed, use of prescribed fires (Pellew 1983), chemical control (Outrum 1970), which can be expensive and seriously affect the environment, and biological control (Kriticos *et al.* 1999), whose success rate has been rather low. All these techniques have been used with variable results, most of them failures.

Kriticos *et al*. (1999) attributed failure of biological control measures on *A. nilotica* in northern Australia to inadequate knowledge of its population dynamics. Similarly, the failure of Tordon® to chemically control the invasion of *A. drepanolobium* in parts of

Laikipia, Kenya, can be ascribed to the ignorance of the tree's population biology and factors that drive it. It is, therefore, essential that the population dynamics of problem species be thoroughly investigated in order to identify weaknesses that may be exploited for effective management (Kriticos *et al*. 1999).

Plant population biology (Harper 1977; Silvertown & Doust 1982), the branch of biology dealing with demography of plants, is an important tool in understanding how plants respond to disturbances (Kriticos *et al*. 1999). The key issues are inputs (births) and outputs (deaths) from a population (Harper 1977; Silverton & Doust 1982; Weigand *et al*. 1999). However, many other factors influence the rates of births and deaths of a population in any given ecosystem (Coe & Coe 1987). These factors should be examined and understood with a view to determining the critical processes that drive plant population dynamics (O'Connor 1996; Kriticos *et al*. 1999; Weigand *et al*. 1999).

## 2.3 SALIENT FEATURES OF BUSH ENCROACHMENT BY *ACACIA DREPANOLOBIUM*

*Acacia drepanolobium* is the dominant species in arid uplands with impeded drainage where it forms nearly mono-dominant stands, especially on black cotton soils (Coe & Beentje1991; Beentje 1994; Young *et al.* 1997; Young *et al.* 1998). Some of the thorns of this species are swollen at the bases, confluencing into large hollow pseudo-galls (hereafter galls), which are occupied by ants from *Crematogaster* and *Tetraponera* species (Young *et al.* 1997; Stanton *et al.* 1999; Palmer *et al.* 2000).

Many herbivores including giraffe (*Giraffa camelopardalis* L.), goats (*Capra hircus* L.) (Young 1987), eland (*Taurotragus oryx* Pallas), elephant (*Loxodonta africana* Blumenbach), Jackson's hartebeest (*Alcelaphus buselaphus jacksoni* Pallas), Grant's gazelle (*Gazella granti* Brooke), and even camels (*Camelus dromedaries*) (personal observations) browse on *Acacia drepanolobium.*

The ecology of *A. drepanolobium* is virtually unknown. Most of the expected responses of *A. drepanolobium* to disturbance by herbivores, fire and harvesting are therefore, inferred from literature reported for other African *Acacia* species that have been studied. A major difference between *Acacia drepanolobium* and many of the African *Acacia* species, referred to in this literature review, stems from the presence in the former of swollen thorns (galls) in which *Acacia* ants live, and its more or less restricted distribution (Beentje 1994).

These factors may imply that *A. drepanolobium* may not respond in a similar manner to other African *Acacia* species studied thus far. *Acacia zanzibarica* (Ross 1979; Stapley 1999) and *A. seyal* var fistula (Ross 1979; Beentje 1994; Young *et al*. 1997) are among other African *Acacia* species with swollen thorns in which ants live.

African *Acacia* species are believed to respond differently to factors such as rainfall, soils, fire, herbivory, and human use that might determine their population dynamics (Ruess & Halter 1990; Pellew 1983; O'Connor 1996). Though it is relatively easy to see how individual *Acacia* species respond to rainfall, there is a paucity of knowledge on how they respond to the other four factors, especially when these factors operate in combination (Young *et al*. 1998). The inadequate knowledge of response of plants to these factors seriously limits our understanding of their dynamics and, therefore, undermines the management that can be formulated for their profitable and sustainable management of such plants (Belsky 1984).

### 2.3.1 Herbivory and *Acacia* species

At the landscape level, the presence or absence of herbivory, especially by large mammals, has been shown to impact significantly on the vegetation structure and composition of many African savanna habitats, e.g. Nairobi National Park, Kenya (Western & Gichohi 1993), Queen Elizabeth National Park, Uganda (Lock 1993), the Seronera Valley, Tanzania (Pellew 1983), and Serengeti-Mara ecosystem (Dublin 1995).

The main defoliation agents in African savanna habitats are herbivores, which differ in their effects on browse plants (Owen-Smith 1988; Dublin 1995). Elephants (Tchamba 1995) and giraffes (Pellew 1983) have especially been reported to have the greatest impact on woody vegetation in savannas. Mega-herbivores, e.g. elephant and giraffe, are expected to have different effects on vegetation compared with medium sized species like eland and hartebeest, which may also have effects different from those of smaller herbivores like impala (Belsky 1984).

The net effects of a combination of all these herbivores on vegetation may also be significantly different, thus changing the path of the population dynamics of certain species (Dublin 1995). This necessitates a separation of the effects of these different herbivore categories in order for a clearer understanding of their individual and collective effects on vegetation to be understood (Young *et al.* 1998).

### 2.3.2 Effects of herbivory on *Acacia* species

At the individual level, many African *Acacia* species that have been studied, have shown compensatory growth in response to defoliation either by herbivores or by clipping (Milton 1983; Teague 1988b; Oba & Post 1999). However, there still exists a large gap in knowledge on how they respond to most mammalian and/or invertebrate herbivores. In addition, only a few species have been studied and the conclusions drawn may be generalisations that do not apply to all species in this genus.

The sensitivity of African *Acacia* species to defoliation depends on the frequency and intensity of defoliation, the phenophase of the plant, location of browsing within the plant, and type of defoliation agent (Teague 1988a). In another example, Du Toit *et al.* (1990) reported that shoot extension rates were maintained under long-term browsing pressure in *A. tortilis*. Time of defoliation is also a factor (e.g. *A. tortilis,* Milton 1988). However, this study was done in Southern Africa, a region with a unimodal rainfall pattern, which is quite different from the often bi- or tri- modal patterns experienced in many parts of the East African savanna (Pratt & Gwynne 1977; McClanahan 1996). Pellew (1983) also reported compensatory forage production in *A. tortilis, A. xanthophloea* and *A. hockii* after clipping.

Therefore, both clipping and defoliation through herbivory may lead to compensatory growth in African *Acacia* species. Teague (1988c) concluded that plants could compensate for defoliation in the lower but not in the upper half of the canopy, a phenomenon attributed to the dominant shoots in the upper half of the canopy (Pellew 1983; Teague & Walker 1988).

However, compensatory growth of *Acacia* species, in response to defoliation cannot be without cost to the overall growth of the plant (Harper 1977; Salisbury & Ross 1985). Milton (1988) reported an inverse relationship between frequency of shoot pruning and increment in the basal area of *A. tortilis*.

The removal of tissue through defoliation may also result in a host of altered physiological processes and allocation patterns in the plant. The responses include, *inter alia*, increased photosynthetic rates, resulting from increased irradiance, relocation of substrates from elsewhere, prolonging active life of remaining photosynthetic tissues, and activation of remaining meristematic tissues (Salisbury & Ross 1985). All of these changes have an important bearing on the dynamics of the species because some of the changes may influence future browsing patterns. Du Toit (1990a) proposed a positive feedback on heavy browsing of *A. tortilis* and *A. nigrescens* by giraffe.

Apart from growth and forage production, defoliation of *Acacia* species by herbivores can influence most other stages of a plant's life cycle, e.g. dispersal, germination, seedling establishment, growth and mortality (Harper 1977; Coe & Coe 1987; Mucunguzi 1995). Many indehiscent *Acacia* species depend on mammalian herbivores for their seed dispersal (Lamprey *et al*. 1974; Coe & Coe 1987; Miller 1995), but individual plant species may be dispersed by a large number of browser species. This suggests a lack of species-specificity in dispersal, but a major determinant of which *Acacia* species are dispersed by a browser is the thickness of the seed testa and ability of the seed to withstand chewing (Coe & Coe 1987). Germination and establishment may, therefore, also depend on how and where seeds are dispersed (Fenner 1986).

The extent to which herbivores may influence seed production, because of curtailed flower production, is not clear. Coe & Coe (1987) suggested that pollination success of *Acacia* flowers is generally low, and therefore herbivory is unlikely to have a significant effect (O'Connor 1996). The pod: flower ratio in many African *Acacia* species is low (Ross 1979; Du Toit 1990b).

Du Toit (1990 b) also reported that most African *Acacia* species bear sterile flowers, and hence herbivory on them may be of little consequence to eventual seed production. However, if herbivory is intense and most herbage is defoliated, flowering may not take place and consequently no seed production may occur. Hence, the level of herbivory may be important in indirectly determining the degree of seed production. Du Toit (1990b) suggested that giraffes may be important in the pollination of *A. nigrescens*, thus implying that other herbivores too may be important pollen vectors of African *Acacia* species, although he provided no data.

Seedling recruitment is probably the life-history stage most vulnerable to browsing (Coe & Coe 1987; Miller 1984; Miller & Coe 1993; O'Connor 1996). Seif el Din & Obeid (1971) showed that survival and shoot length of young *A. senegal* seedlings was depressed by simulated browsing only for the first 38 days. Prins & Van der Jeugd (1993) reported that *A. tortilis* in Manyara National Park, Tanzania, had experienced only three recruitment episodes in the last century, which corresponded with crashes in the impala population. This suggests that impala could have played a critical role in limiting recruitment. This view is supported by results of Belsky (1984) in the Serengeti. Sheep can limit the recruitment of *A. karroo* and A. *nilotica* in South African grassland (Kanz 2001). Herbivores can also significantly impact recruitment via vegetative regeneration or propagation in some *Acacia* species. Okello (1996) found that herbivory had stunted the growth of *A. etbaica* in the communal rangelands of Laikipia, thus limiting their regeneration.

### 2.3.3 Defence mechanisms of *Acacia* species to herbivory

Because defoliation has a direct effect on many savanna woody species, many African *Acacia* species have evolved mechanisms for defending themselves against defoliation, especially by mammalian herbivores (Owen-Smith 1982; 1993; Young 1987; Milewski *et al*. 1991; Madden & Young 1992; O'Connor 1996). The defences can be either physical, e.g. thorns and spines, or chemical (Owen-Smith 1983; 1993; Coe 1983). *Acacia drepanolobium* is among a group of unique *Acacia* species that have ants, which are believed to aid in defence against herbivory (Madden & Young 1992; Young *et al.* 1997; Stapley 1998; Stanton *et al.* 1999).

The defence mechanisms have been hypothesised in terms of resource availability or carbon-nutrient balance (Bryant *et al.* 1983; Coley *et al.* 1985). Generally, species growing on nutrient rich substrates, (e.g. African *Acacia* species), tend to rely on physical defences and rapid growth, while those on nutrient poor soils invest mostly in carbon-based chemical defences, though not exclusively so (Coley *et al*. 1985).

Herbivory can induce an increased level of spinescence (Young 1987; Milton 1988; Milewski *et al.* 1991). Increase in thorniness of new shoots can decrease the bite rate of browsers (Cooper & Owen-Smith 1986). The converse may be true, though no empirical experiments have been reported. These structural adjustments have important implications because these are permanent, at least over that growth period or season (O'Connor 1996).

Herbivory, on its own, may not be critical in determining the survival and establishment of *A. drepanolobium,* because it is not the most preferred of the *Acacia* species. However, herbivory in conjunction with fire and harvesting may significantly influence the population dynamics of such species (Pratt & Gwynne 1977; Norton-Griffiths 1979; Gichohi *et al.* 1996; Young *et al.* 1998).

### 2.3.4 Fire and *Acacia* species

Fire is one of the most potent forces that may shape the structure of African savanna ecosystems (Vesey-Fitzgerald 1960; Heady 1966; Pratt & Knight 1971; Edroma 1984;

Stander *et al.* 1993; D'Odorico *et al*, 2005). The degree to which fire influences the structure and functioning of the woody layer depends on the frequency and intensity of fire, and the availability of fuel, which is determined by herb-layer production (Heady & Heady 1982; Pellew 1983; Dublin 1995) and intensity of grazing (Heady 1978) and also the type of fire (Trollope & Trollope 2002), whether a back fire or a head fire. In southern Africa, experiments have shown the season of burning to also have a significant influence (Pratt & Gwynne 1977). In recent times, scientists in Africa have begun to pay more attention to fire behaviour (Trollope & Trollope 2002).

Fires have historically been an important ecological process in the East African savanna ecosystems influencing herbaceous composition, forage quality and density of woody species (Pratt & Gwynne 1977; Lock 1993; McNaughton & Banyikwa 1995). Fires were common in these ecosystems until the late 1950's (Heady 1978). However, fires have become infrequent in ranching areas such as the Laikipia rangelands because they are considered inappropriate tools for range management and environmentally incorrect by the range managers (Mwihuri 1998). The decline in fire frequency, coupled with a reduction in the abundance of browsing herbivores, has apparently resulted in an increase of woody vegetation of the Laikipia ranching region (Okello 1996), which is now threatening to be a serious bush problem (Ng'ethe *et al.* 1997).

The effects of fire on African savannas are not well-understood (Gichohi *et al.* 1996), with the result that the desired objectives of the use of fire are often not achieved (Wein & Edroma 1986). Similarly, the interactions of fire with climate, soil and herbivory are poorly understood (Hobbs & Grimmingham 1987; Bock *et al* 1995; Whelan 1995).

Reduction of bushiness by killing trees and shrubs is one of the major effects of fire in savanna ecosystem (Thomas & Pratt 1967; Pratt & Knight 1971; Tchie & Gakahu 1989). Death of browse species is generally dependent on the species' intrinsic adaptation to fire (Pratt & Gwynne 1977) and, the frequency and intensity of fire (Pellew 1983, Dublin 1995). The extent of top-kill and complete mortality of the ligneous layer is inversely related to size (Pratt & Knight 1971), though Tchie & Gakahu (1989) found that a prescribed fire killed trees irrespective of heights at Kiboko, Kenya.

Browsing following a fire maintains a coppicing plant in a short state thus making it more susceptible to subsequent fires (Trollope 1974; Ruess & Halter 1990). Heavy browsing by small ungulates (e.g. impala and Grant's gazelle) can also maintain woody plants less than a meter tall in a short state (Belsky 1984), thus prolonging the period of a plant's susceptibility to fire. Similarly, browsing of seedlings keeps them dwarf, and exposes them to fire damage (Okello 1996). A classic case of the fire-herbivory effect on *Acacia* species was reported by Pellew (1983), in which elephant damage and giraffe browsing in the Serengeti plains constrained the recruitment of *A. tortilis* and, in conjunction with fire, was projected to lead to the demise of the woodlands.

### 2.3.5 Harvesting of woody species by humans

When woody plants are harvested for fuelwood or building material, the regenerating vegetation will often be more vulnerable to fires. Harvesting of *Acacia* trees for various uses is very common in the African savannas (Tietema *et al.* 1991; Rosenschein *et al*. 1999). However, not all African *Acacia* species coppice after harvesting (e.g. *A. etbaica*, pers. observation), implying that heavy harvesting of such species may lead to their local extirpation.

Most of the trees and shrubs harvested from Laikipia rangelands are used for fuelwood production and as building material (Young & Francombe 1991). However, the impact of this activity on the general ecosystem is not known, neither is it based on any sound scientific background. Okello (1996) called for a scientific approach to the use of the abundant browse resources of the Laikipia rangelands. The available biomass is one of the key issues that should be determined before such resources are utilized (Lusigi 1984; Deshmukh 1992; Rosenschein *et al*. 1999). In addition, the pattern of harvesting (inter-harvesting period, and whether clear or selective felling is to be used) should also be determined for sustainable flow of biomass (Kennedy 1998; Smith *et al*. 1999).

Harvesting of indigenous trees and shrubs for the provision of building materials and fuelwood is a noble idea (Little 1972; Rosenschein *et al.* 1999; Smith *et al.* 1999), especially because the introduction of plantation forestry to replace the same has largely failed in East Africa (Young & Francombe 1991; Kennedy 1998). Conventional agroforestry approaches have met with little success because of inappropriate species, long cropping intervals, and inadequate husbandry techniques used by the harvesters, mostly the rural poor (Young & Francombe 1991). Most studies on sustainable harvesting of trees have dealt with plantation species, often in woodlots. However, little attention has been paid to the sustained cropping and improvement of indigenous trees and shrubs for fuel-wood production. Most indigenous trees and shrubs need minimal supervision and husbandry (Kennedy 1998). Young & Francombe (1991) proposed *Tarchonanthus camphoratus* (leleshwa) as a candidate for sustained charcoal production.

However, there is a need to base harvesting on sound scientific knowledge (Deshmukh 1992) in order to ensure long-term sustainability (Young & Francombe 1991). Of critical importance are the rates of regrowth and the degree of mortality arising from harvesting, the new biomass accumulation rates, and the effects of regrowth on the neighbouring plants. These have not been investigated for many promising African *Acacia* species.

### 2.3.6 *Acacia* Ants

A unique feature of *A. drepanolobium* mentioned earlier is the presence of swollen thorns or pseudo-galls that house *Acacia* ants. Ant-acacia relationships have been known for a long time (Janzen 1966; Hocking 1970). There are various types of relationships, ranging from symbiosis to parasitism (Stanton *et al*. 1999). In *A. drepanolobium*, four ant species - *Crematogaster mimosae, C. nigriceps, C. sjoestedti* and *Tetraponera penzigi* - (Young *et al*. 1997; Stapley 1998; 1999; Stanton *et al*. 1999, Palmer *et al*. 2000) are thought to be obligate (Young *et al*. 1997).

The role of these ants on *A. drepanolobium* population ecology has been a subject of speculation, but they are believed to play an important role in defending the tree against herbivory (Madden & Young 1992). In recent years, speculation and interest has increased on how four different ant species live on a seemingly uniform resource (Stanton *et al*. 1999; Palmer *et al*. 2000). So far, the influence of these ants on the population dynamics of *A. drepanolobium* trees is still unclear.

Though many hypotheses on the coexistence of these ants have been proffered (Young *et al*. 1997; Stanton *et al*. 1999; Palmer *et al.* 2000), none are any closer to explaining the existing relationships and how these ants influence the dynamics within the *A. drepanolobium* ecosystem. It is to be expected that these ants probably play an important role in the population dynamics of *A. drepanolobium* if only because they are useful in defending the tree against mammalian herbivory.

From the foregoing, it is therefore necessary to understand the impact of the interactions of livestock, wildlife and fire, and their effects on the range they share, for enlightened and sustainable management of the wildlife-rich Laikipia rangelands. This need also arises from three other reasons. Firstly, Laikipia rangelands in the Rift Valley area of Kenya has probably the highest biomass of wildlife outside protected areas in Kenya, and more than 80% of Kenya’s wildlife is currently found outside parks (Western & Henry 1979). This area is also a premium livestock ranching region, which maintained a large wildlife biomass even during the period of escalated wildlife poaching in the 1970's and 1980's.

Secondly, because wildlife can provide the much-needed additional revenue (eco-tourism and game ranching), a strategy of mixed ranching (wildlife and livestock), may be economically optimal and help maintain biodiversity (Hopcraft 1990). There is a need to justify the continued existence of wildlife in these ranches, and this requires well thought out policies that can only be negotiated if a sound body of knowledge is made available.

Thirdly, certain areas of Laikipia with *A. drepanolobium* are undergoing bush encroachment, which may threaten the herb-layer production. Measures to control this encroachment on a sustainable basis are needed, but these must be based on a sound knowledge of the ecology of the species.

There have been quite a few studies of experimental manipulation of cattle and various guilds of wildlife e.g. (McNaughton 1979; Belsky 1984; Dublin 1995; McNaughton & Banyikwa 1995) in savanna ecosystems. There is however, a paucity of knowledge about the interactions between wildlife, cattle and vegetation, and especially the effects of animals on vegetation (Young *et al*. 1998). In addition, there have been very few experimental approaches to the study of interactions of cattle, wildlife and vegetation in African savannas (Young *et al.* 1998).

This study, which is part of a larger project (Kenya Long-term Exclosure Project – KLEE, Young *et al.*1998) was designed with the goal of addressing the effects of different types of herbivores (Cattle, mega-herbivores, and wildlife) on the population dynamics of *A. drepanolobium,* the most dominant tree in the ecosystem. To provide a more comprehensive picture of the factors affecting the population dynamics of *A. drepanolobium*, a prescribed burning was undertaken and the rate of biomass gain and biomass yields of *A. drepanolobium* were investigated. A preliminary investigation on the effects of *Acacia* ants on its population dynamics was also done.

## 2.4 OBJECTIVES OF THE STUDY

The overall objective of this study was to understand how herbivores, fire and harvesting can influence the population dynamics of *Acacia drepanolobium* in the rangelands of Laikipia Kenya.

*The specific objectives of this study were:*

1. To determine how herbivory by large mammals affect populations of *A. drepanolobium* in the black cotton ecosystem, especially the response of *A. drepanolobium* to different groups of herbivores with respect to tree growth rates, survival/mortality, and induced defences.

2. To understand the seed ecology of *A. drepanolobium* by:

   a) Determining the degree of flowering and seed production of *A. drepanolobium*;

   b) Investigating the effect of bruchid beetle infestation on *A. drepanolobium* germination rates; and

   c) Determining the seedling establishment and survival of *A. drepanolobium* among different soil types.

3. To quantify the effects of fire on the demography of *A. drepanolobium*:

   a) Determine the effects of fire on *A. drepanolobium* demography (growth in height, diameter, and survival);

   b) Document changes in the herb layer species composition and cover before and after a burning and mowing.

4. To develop predictive equations for estimating yield of woody biomass and of charcoal, and to establish the rate of regrowth of coppicing stands through chrono-sequence analysis.

5. To examine how acacia ants affect the population dynamics of *A. drepanolobium* with respect to the following:

   a) Quantify ant distribution in an *A. drepanolobium* ecosystem;

   b) Document ant turn-over in a population of *A. drepanolobium;* and

   c) Monitor the response of the host trees to the presence of the different ants particularly in relation to growth, changes in canopy volume and structure, herbivory by mammals, flowering, seed production, and tree mortality.

# 3 CHAPTER THREE: STUDY AREA AND SPECIES

## 3.1 STUDY AREA

This study was carried out at Mpala Research Centre in Laikipia District of north-central Kenya. The study site is located in the south-western corner of the property (0° 18' 30" N, 36° 54' 28" E) at an altitude of 1800 m above sea level (Fig 3.1). Details of the study area have been documented by Young *et al.* (1998), (see Appendix 1).

The area receives a mean annual rainfall of 500-550 mm (average of 40 years) with a weak tri-modal tendency. Rainfall in the study area is characterised by large spatial and temporal variation (Young *et al.* 1997; 1998) with April to May as the peak rainy seasons and most of the remainder falling between July and November (Fig. 3.2). The total rainfall received from January 1996 to December 1998 was 2097 mm, distributed as follows; 394 mm for 1996, 922 mm in 1997 and 781mm in 1998. The last two years received above average rainfall occasioned by the *El Nino* phenomenon. In the three years two prominent and one weak rainfall peak were evident.

Maximum daily temperatures range from 25°C to 33°C, and minima from 12°C to 17°C. The soils of the study area are black cotton (vertisols) soils (Ahn & Geiger 1988; Taiti 1992; Young *et al.* 1998) derived from volcanic rocks. The soils swell when wet and crack when dry. The topography is generally flat with slopes less than 3%, and the area experiences periodic water logging for up to 14 days during rainy periods and overcast skies. However, the soils also dry out quickly when the sun shines.

### 3.1.1 Vegetation

The woody layer of the vegetation is dominated by *Acacia drepanolobium*, which accounts for about 97% of overstorey tree and shrub density. Other overstorey species include *Rhus natalensis, Grewia similis*, *Grewia bicolor, Scutia myrtina*, *Lycium europaeum* and *Cadaba farinosa*. *Acacia brevispica* ssp. *brevispica, Acacia mellifera* and *Balanites aegyptiaca* are uncommon (Young *et al*. 1997; 1998).

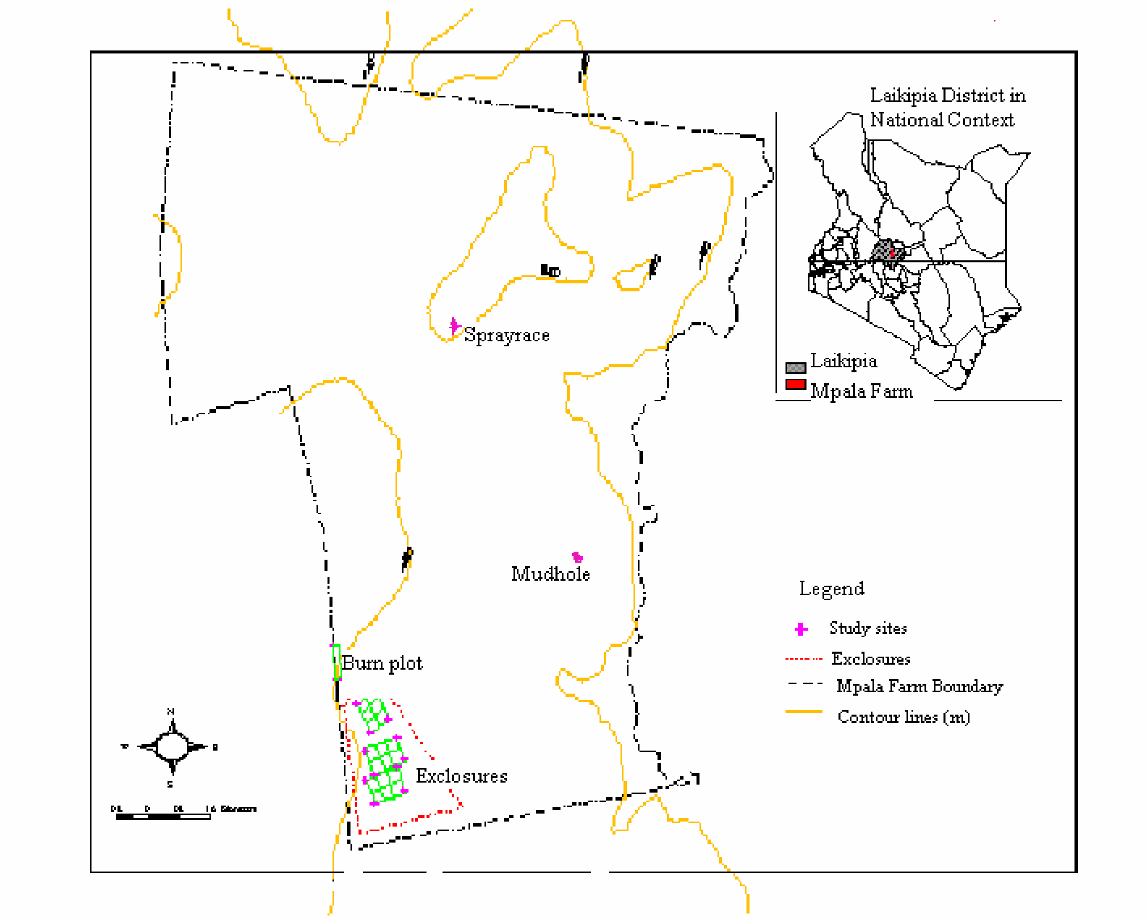

Fig. 3.1 Map of Laikipia district showing the location of Mpala Ranch and the study sites within the Research Centre.

The herb layer is equally simple and dominated by five grasses species. The grasses - *Pennisetum stramineum, Pennisetum mezianum, Themeda triandra, Lintonia nutans*, and *Brachiaria brizantha*, and two forb species (*Aerva lanata* and *Helichrysum glumaceum*) account for more than 90% of the cover (Young *et al*. 1998).

Extensive livestock ranching is the main land-use at Mpala and Laikipia in general, although some ranches concentrate on wildlife tourism or combine both wildlife and livestock enterprises. On many ranches, livestock are kept as the only enterprise though wild animals have access. Livestock stocking rates are low to moderate at Mpala and nearby commercial properties, barely exceeding 8 ha per livestock unit. For Example, Mpala ranch keeps about 2,300 head of cattle (including calves) on its 20,234 hectares (about 8 hectares to a livestock unit).

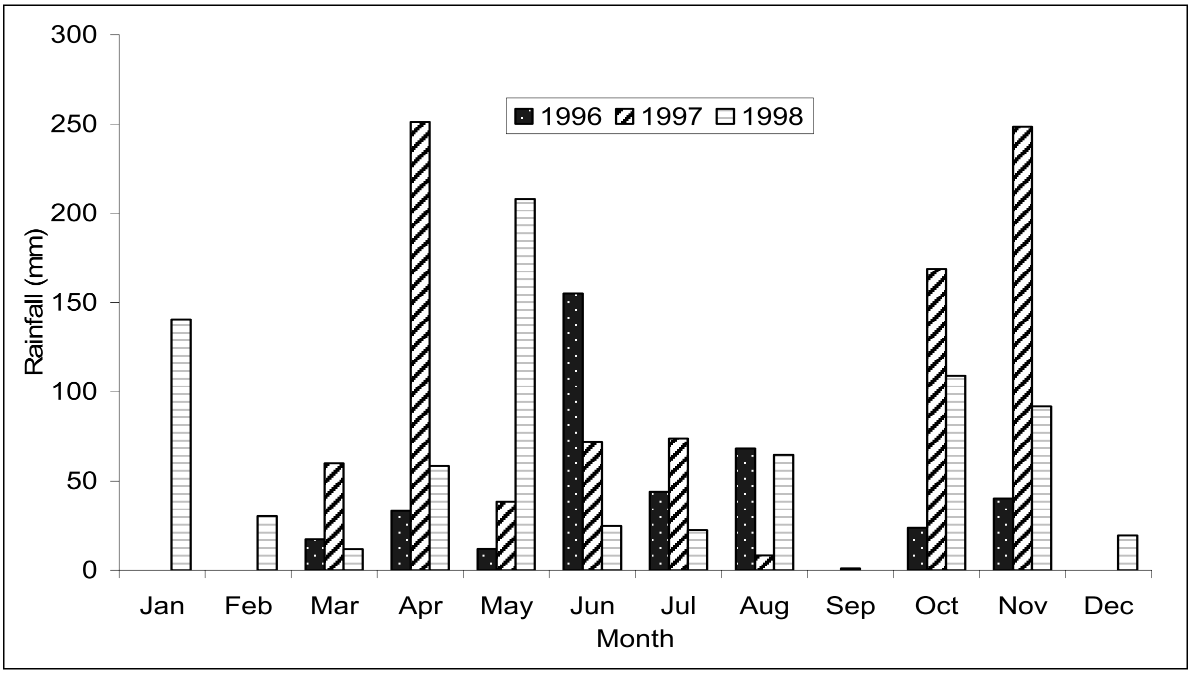

Fig. 3.2 Mean monthly rainfall recorded on the KLEE project at Mpala Research Centre (1996 to 1998). Three recording stations were used, one for each replicate.

The Laikipia ecosystem is an important wildlife area because it has one of the largest herbivore biomasses outside national parks and games reserves in Kenya. Dominant large herbivores (nomenclature by Dorst & Dandelot (1972), Estes (1991), and Kingdon (1997)) in the study area include cattle (*Bos indicus*), Burchell's zebra, Jackson's hartebeest, steenbok, Grant's gazelle, Beisa oryx, elephant, eland, and giraffe (Table 3.1) (see also Young *et al.* 1995; 1997; 1998).

The data indicates that on average, there are more than 500,000 herbivores in Laikipia, translating to about 54 animals per sq.km. Data from Georgiadis *et al*. 2003 indicates there were at least 640,000 herbivores, giving a density of 69 animals per sq.km. These data have not included smaller wildlife and the carnivores (which are secretive).

Table 3.1 Estimated wildlife and livestock numbers in Laikipia District, from aerial surveys using one total and two sample counts in the months of September 1996, February 1997 and June 1997

| Species | Total count Sep, 1996 | Sample count Feb, 1997 | S.E. | Sample count June, 1997 | S.E. |
|---|---|---|---|---|---|
| Burchell's zebra | 33,388 | 35,859 | 4,109 | 31,797 | 4,251 |
| Impala | 6,590 | 8,436 | 1,328 | 8,748 | 1,566 |
| Grant's gazelle | 4,055 | 6,997 | 974 | 7,602 | 1,228 |
| Thomson's gazelle | 4,471 | 5,150 | 1,060 | 5,846 | 1,594 |
| Eland | 3,393 | 3,667 | 699 | 5,329 | 1,509 |
| Buffalo | 1,915 | 2,655 | 761 | 1,937 | 514 |
| Elephant | 2,392 | 1,847 | 450 | 3,435 | 860 |
| Hartebeest | 1,729 | 2,131 | 414 | 1,825 | 408 |
| Giraffe | 1,647 | 1,856 | 405 | 1,498 | 381 |
| Oryx | 734 | 1,385 | 364 | 1,584 | 482 |
| Waterbuck | 571 | 621 | 160 | 688 | 180 |
| Gravy's zebra | 837 | 870 | 216 | 723 | 287 |
| Gerenuk | 178 | 319 | 111 | 378 | 132 |
| Subtotal wildlife | 61,900 | 72,618 | | 71,390 | |
| Cattle | | 163,119 | 13,544 | 163,119 | 11,530 |
| Sheep & Goat | | 192,585 | 20,871 | 192,585 | 19,018 |
| Camel | | 2,371 | 596 | 2,371 | 1,283 |
| Donkey | | 2,726 | 512 | 2,726 | 457 |
| Subtotal livestock | | 360,801 | | 360,801 | |
| Total herbivores | | 433,419 | | 398,542 | |

Source: Department of Resource Surveys and Remote Sensing and Mpala Research Centre.

Wildlife numbers presented in Table 3.1 are for Laikipia District. All the species in the table are found at Mpala Research Centre.

Another feature of the study area and this ecosystem in general is the presence of numerous glades. Glades are tree-less patches of land, have a high level of nutrients (Young *et al.* 1995), and are preferentially used by wild and domestic herbivores. Most glades are less than one hectare though some are much larger.

## 3.2 MATERIALS AND METHODS

### 3.2.1 The study species – *Acacia drepanolobium*

*Acacia drepanolobium* (commonly known as the whistling thorn) is the dominant species in arid uplands with impeded drainage where it forms nearly mono-specific stands especially on black cotton soils (Young *et al*. 1997; Young *et al.* 1998). It has a wide distribution and can be found in the rangelands of Sudan, Ethiopia, Somalia, Kenya, Tanzania, Uganda, and Zaire. Its altitudinal range is 600 to 2550 m above sea level (Coe & Beentje1991; Beentje 1994).

*Acacia drepanolobium* is a shrub or a tree that grows to a height of 7.5 m but maximum height averages 3.5 m over much of its range. It is either a short robust tree or a slender tree with a rounded canopy. Its bark is black, rough, and fissured. The tree remains green through most of the rainy and dry season, although the leaves may dry out during prolonged droughts. *Acacia drepanolobium* has pairs of long and narrow stipular spines (hereafter also referred to as thorns) that grow to 7.5 cm long, but average 3.5 cm in many areas. Some thorns have swollen bases that confluence into large hollow pseudo-galls (hereafter galls), which are red when young and fade to black and grey-white when old.

The swollen thorns are usually longer than their non-swollen congeners. Four ant species, *Crematogaster nigriceps*, *C. sjoestedti, C mimosae*, and *Tetraponera penzigi* (Madden and Young 1992; Young *et al*. 1997) occupy these swollen thorns. These ants may play a much bigger role in the ecology of *A. drepanolobium* than previously assumed (Stanton *et al*. 1999). Casual observation suggests that the ant species are distributed vertically among trees of different tree heights (Young *et al.* 1998; Stanton *et al.* 1999). The architecture of the trees inhabited by different ant species also looks different (Stanton *et al*. 1999).

*Acacia drepanolobium* is browsed by a large number of mammalian herbivores including giraffe, eland, elephant, Jackson's hartebeest, Grant's gazelle, goats and camels (*Camelus dromedaries*). Baboons (*Papio anubis*) and Patas monkeys *(Cercopithecus (Reythrocerbus) patas*) are also frequent visitors, eating the ants in the swollen thorns, gums exuding from the trees as well as new shoots (pers. observation). However, its utilization by herbivores is hampered by the presence of ants that live in its galls. Together with the thorns (Milewski *et al*. 1991), the ants are believed to ward off herbivores by their stings and bites and to irritate feeding herbivores (Madden & Young 1992; Young *et al.* 1997).

### 3.2.2 Experimental layout

A large level tract of acacia wooded grassland of several hundred hectares on the black cotton soils, was selected for the study. This site had no evidence of recent burning. Three replicates of four-hectare plots (200 m x 200 m) for each treatment arranged as a randomised block design were selected. The treatments Fig. 3.3) were:

1) Full fencing to exclude all large herbivores (three replicates).

2) Full fencing, but cattle allowed periodic grazing (three replicates).

3) High single-strand electric fencing to exclude elephants and giraffes only (three replicates).

4) As in # 3, but cattle also excluded (three replicates).

5) Unfenced, cattle allowed periodic grazing (three replicates)

6) Unfenced, cattle are not allowed to graze (three replicates). The electric fence barriers have proved to be effective in excluding wildlife in many ranches in Laikipia (Thouless & Sakwa 1995).

Three types of herbivore barriers were used in the main experiment to examine the effects of different types of herbivores on the population of *Acacia drepanolobium*:

1. The 2.3 m wildlife fence is eleven strands of bare wire, alternating live and ground. Every second, a burst of 6-7,000 volts is sent through the live wires via a battery charged by a solar panel. The lower nine wires are 16 cm apart and the spacing for the upper two is 32 cm. The lowermost (ground) wire is at ground level. To minimize shorting of the lowest electric wire, the area along the bottom of the fence is kept free of vegetation by slashing and by regular applications of Round-up® on calm days during the growing seasons using a backpack sprayer. In addition, any higher tree branches growing into the wires are cut back regularly. In three of the plots enclosed by this fence, there are 1.5m wide gates that can be opened to allow entry by cattle.

2. The mega-herbivore fence (also called a ‘dingle-dangle’ fence) consists of a single live wire 2 m off the ground, and two ground wires. One ground wire is located 32 cm above the live wire. The other runs along the ground, 60 cm outside the plot (to increase the chances that an elephant or giraffe will be standing on it when contacting the live wire). Along the live wire, there are single wires (‘dingle-dangles’) 50 cm long hanging down every 50 cm. This fence is not cleared for vegetation, except branches near the upper wires.

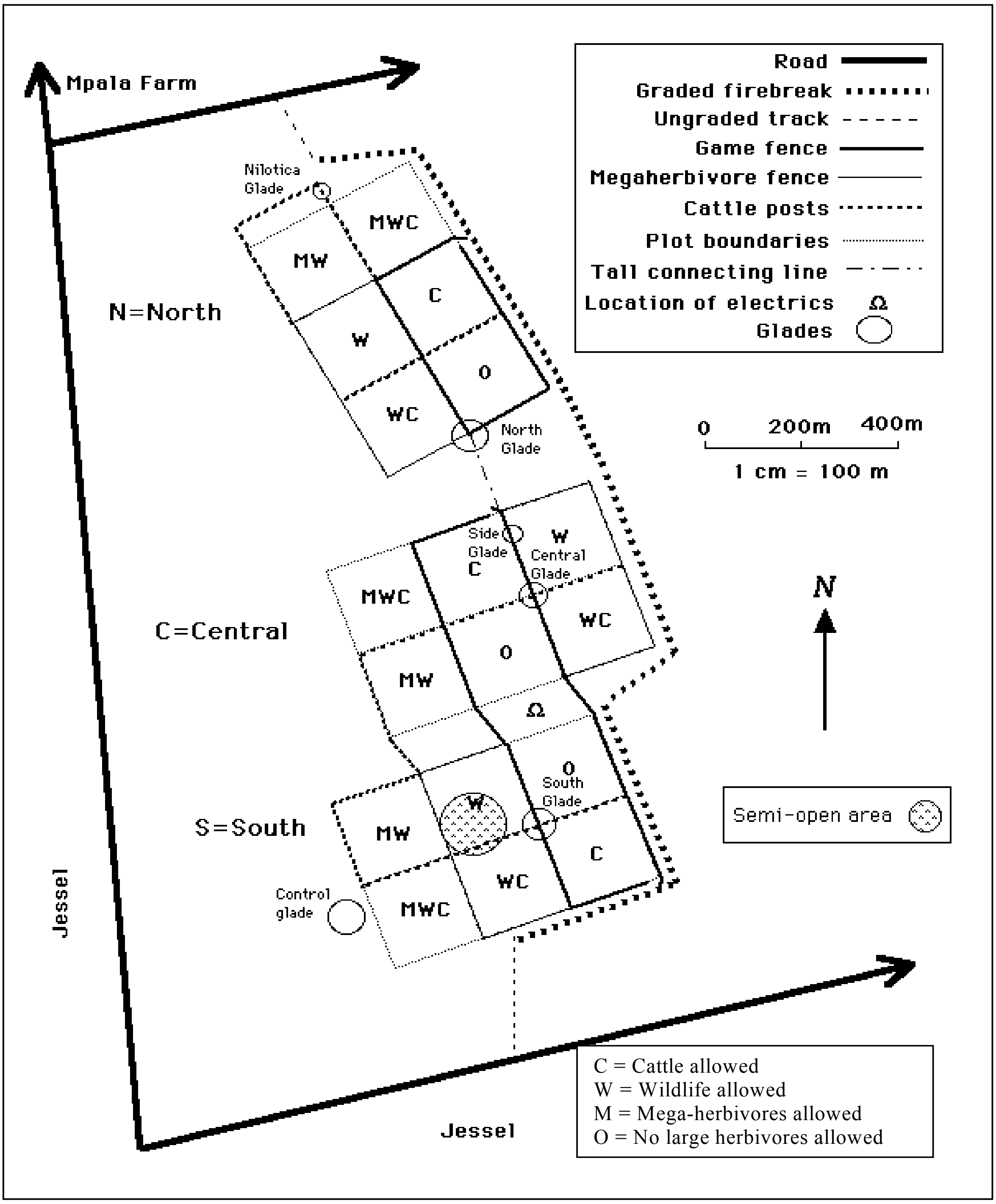

Fig. 3.3. Schematic layout of the KLEE experimental plot. Letters in each plot indicate herbivore type allowed in. Each plot is 200 X 200 m (4 ha). Total experimental area is 72 ha.

3. The cattle barriers are visual. Every 10 m, there is a short post (60 cm high) painted red on the cattle exclusion side. All cattle on the property travel in discrete herds of ~100 head and are accompanied by individual herders on foot. The cattle herders and the person documenting the cattle run use the painted post markers to ensure that cattle do not enter excluded areas.

The cattle are allowed to graze on a controlled schedule, largely following the overall grazing schedule of Mpala ranch. The schedule is flexible where animals are taken to graze in different parts of the ranch depending on the condition of the range. A modification used in the cattle plots is that animals graze for a maximum of two hours, for three consecutive days at most. The number of cattle and the duration of such grazing (in minutes) are quantified for each cattle 'run' inside the plots. Because there are no other large mammals inside the wildlife fences, a physical barrier is used to separate between areas where cattle are allowed or excluded. This is a single electrified wire 60 cm off the ground, attached to short posts. The area below this wire is cleared of vegetation.

Specific methods and statistical analysis used in each chapter of the study are presented in the respective chapters. Detailed date collection for the different objectives of the study is also presented separately in each chapter.

# 4 CHAPTER FOUR: RESPONSE PATTERNS OF *ACACIA DREPANOLOBIUM* TO DIFFERENT HERBIVORE TREATMENTS

## 4.1 CONTEMPORARY CONCEPTS OF MANAGING RANGELANDS

Management of arid and semi-arid rangelands is undergoing re-evaluation worldwide (Ostfeld *et al.* 1997; Young *et al*. 1998; Herlocker 1999). The way in which the dynamics of rangelands or savannas are viewed, especially the conceptual basis and techniques, has undergone a drastic rethinking over the last 20 years (Behnke and Scoones 1992). Mainstream concepts of range management were derived from experiments in the United States of America rangelands, with plant succession, carrying capacity and range condition as guiding principles (Odum 1959; Humphrey 1962; Weaver & Clements 1966, Heady 1976; Behnke & Scoones 1992). The paradigm arising out of this thinking is the 'equilibrium concept' (Walker *et al.* 1981; Belsky 1994), and form the 'mainstream' thinking in range management (Sandford 1983).

However, the concept of equilibrial forces has been criticised as flawed, especially with respect to African rangelands (Behnke & Scoones 1992), and a new paradigm of non-equilibrium concept has been espoused (Ellis & Swift 1988; Behnke & Scoones 1992). Debate on which paradigm is most appropriate to the management of African rangelands and the relative importance of the forces driving the function and structure of these rangelands is still on-going. Inconsistent and sometimes contradicting evidence from research coupled with 'too many' variables during research have so far prevented concurrence and it will be a while before consensus is reached on a practical and profitable concept. Range managers, especially in Africa have to adjust and adopt new strategies of managing their range, not because of the emerging paradigms, but based on increasing demands for more and better quality products and services including sustainable conservation and utilization of the rangelands.

Imminent changes on how these rangelands are managed stem partly from the current systems of land use being: i) traditional pastoralism (Heady 1975; Pratt & Gwynne 1977), ii) commercial ranching, which may or may not include wildlife (Okello 1996), and iii) wildlife conservation, especially game parks and reserves (Western 1996). Other uses include their role as catchment areas, sources of fuelwood, especially charcoal, and mining of minerals (Smit *et al*. 1996).

### 4.1.1 Livestock versus wildlife

As the profitability of livestock production becomes increasingly marginal mainly due to increased costs of production and possibly due to poor management (Butterworth & Lambourne 1985; McClanahan & Young 1996), the value of wildlife has increased. Managers are using wildlife as a source of additional income, especially for tourism on commercial ranches. Many wildlife conservancies are being set up even in the communal areas of Laikipia. It may be unrealistic to expect that ranchers will completely shift from livestock ranching and concentrate (their management) on wildlife. A more likely occurrence is where both are managed on the same piece of land, a situation that already prevails on many ranches.

Livestock and wildlife share much of their respective habitats in most arid and semi-arid lands (Owaga 1976; Shaw 1985; Mbuvi & Croze 1986; Nyeki 1993). This fact alone necessitates a detailed understanding of the ecology and dynamics of these ecosystems, which is critical to further long-term development, management and conservation (Bourliere 1983; Noble 1986). Specifically, there is a need for a better understanding of the interactions between livestock and wildlife, and their effects on the rangeland ecosystem in order for acceptable and practical management options and policies to be realised.

Recent studies in Kenya show that there are probably more individuals of large indigenous herbivores in multiple-use lands (e.g. ranches in rangelands) than in parks and reserves (Western & Gichohi 1993; Herlocker 1996; DRSRS & MRC 1998). The continued existence of wildlife on ranches will be subject to informed management (Young *et al.* 1998). The needs of landowners and those of wildlife will have to be met in a delicately negotiated balance amongst conservationists, landowners, and policy makers. This can only be done after a sound body of knowledge with practical management options are made available and ecologists have a role to provide this information.

Interactions between livestock and wildlife in many African savannas are often viewed negatively (Caughley 1986; Prins & Douglas-Hamilton 1989). Wildlife are frequently blamed for being destructive to infrastructure, consuming much of the forage, and acting as a reservoir of diseases, e.g. tick-borne diseases like East Coast Fever (Mbuvi & Croze 1986). The presence of wild herbivores inevitably attracts predators, which also predate on domestic livestock (Ogada 2000).

There is evidence that many wildlife species may actually have beneficial effects when kept together with livestock. Examples include reduction in brush cover when large browsers are kept (Moore 1974; Leuthold 1996; Smit *et al*. 1996), and the clearing of dry stubs of grass by zebras, an action that allows for fresh growth when rains fall (McNaughton 1986). To a large extent, the effects of interactions between livestock and wildlife would depend on their respective densities and the land's carrying capacity. At high stocking rates, livestock in the absence of wildlife can impact negatively on the range (O'Connor 1985). High densities of wildlife have also been shown to have profound effects and impacts on the structure and function of savannas (Moore 1974).

A strategy of mixed ranching of wildlife and livestock is attractive because wildlife have increased in value on account of eco-tourism and controlled harvesting, and because it may allow range managers to optimise revenue while maintaining biodiversity in the midst of declining livestock productivity (Western & Henry 1979).

### 4.1.2 Kenya Long-term Exclosure Experiment (KLEE)

African *Acacia* species are among the dominant woody species in savanna ecosystems in Africa and are, therefore, of immense importance to the structure and functioning of savanna ecosystems (Ross 1979; Beentje 1994). Understanding their biology and how this is impacted by different categories of herbivores acting singly or together, is of theoretical and practical significance to rangeland managers, planners, and researchers.

As a step towards understanding the effects of interactions between livestock and wild herbivores on woody trees in savannas, the population dynamics of *A. drepanolobium* under different herbivore treatments was studied in Laikipia, Kenya. Experimental manipulations in the field (Young *et al*. 1998) were used to tease out the causative factors of the observed responses. *Acacia drepanolobium* is an ideal species for such a study because: 1) it is the dominant woody species over large areas of Laikipia; 2) it is largely restricted to black cotton soils; 3) it occurs in seemingly mono-specific stands of similar maximum heights; 4) it coppices readily when burned or harvested; 5) many ranchers in Laikipia claim it has become a bush problem; and 6) it hosts at least four species of *Acacia* ants that gives rise to an interesting ecological relationship between the ants and the trees.

This study is part of the larger KLEE initiated in September 1995 to study the interactions between livestock and wildlife in this ecosystem (Young *et al*. 1998).

### 4.1.3 Hypotheses on the effects of livestock - wildlife interactions on *Acacia drepanolobium*

Mega-herbivores like elephants and giraffes were expected to have significant effects on the population dynamics of *A. drepanolobium.* For example, elephants are known to be destructive of trees and shrubs (Dublin 1995), while giraffe browsing pressure can significantly reduce their vigour (Moore 1974; Pellew 1983). Therefore, treatments with mega-herbivores were expected to have greater mortality rates than treatments with other groups of herbivores. Compensatory growth has been reported in some African *Acacia* species after being browsed (O'Connor 1996), hence effects of mega-herbivores on tree growth rate and utilization were expected to be significant. Belsky (1984) showed that small browsers like impala could impact the population dynamics of woody species significantly, therefore, herbivores like Grant's gazelle, eland and hartebeest, which use this ecosystem (Young *et al.* 1998), were also expected to significantly impact on *A. drepanolobium* population dynamics. The response of induced defences by spines of *A. drepanolobium* due to herbivory by mega-herbivore is also expected to be greater than that by the other herbivore categories (Young 1987; Milewski *et al.* 1991; Stapley 1998).

Cattle consume very little browse in Laikipia rangelands (Okello 1996) and their impact on growth and mortality was therefore expected to be minimal or indirect, while the impact of other wildlife species should be greater than that observed in cattle treatments. Treatments without any herbivores greater than 5 kg were expected to respond similarly to those with cattle, though indirect effects that may be ascribed to cattle will be missing. The expected indirect effects include reduced competition for growth resources from the herb layer because of grazing and increased fertility of the soil from cattle dung.

## 4.2 OBJECTIVE OF INVESTIGATION

The aim of this study was to use experimental manipulations in the field to establish how populations of *A. drepanolobium* are affected by different categories of large herbivores in the black cotton soils of Laikipia Kenya.

The specific objectives were to:

1. Determine the extent to which different categories of large herbivores utilize the foliage of *A. drepanolobium* and the effect of this utilization on the tree.

2. Investigate the influence of herbivores on the demography of *A. drepanolobium* with respect to flowering, seed production, seedling establishment, tree growth rates and survival.
3. Explore how herbivory by large herbivores may influence the physical defences (spine production) of *A. drepanolobium*.

In addressing the above objectives, the underlying hypothesis was that large herbivores affect the population dynamics of *A. drepanolobium* in a consistent and predictable manner. The large herbivores whose effects were of interest include:

Mega-herbivores (M) – elephant and giraffe. There two were expected to browse the Acacia drepanolobium trees heavily in treatments in which they were allowed, and that these heavy browsing would manifest itself in several aspects of the tree's population dynamics – growth, reproduction and mortality (i.e. slow growth, reduce reproduction and enhance mortality)

Wildlife (W) – browsing wildlife including eland, Grant's gazelle, hartebeest and bush buck: These were also expected to impact the population dynamics of the tree, but not as heavily as the Mega-herbivores.

Wildlife (W) – grazing wildlife including zebras were not expected to impact the population dynamics of the tree directly, but could do so indirectly.

Cattle – being grazers, cattle were not expected to have any direct effects on the population dynamics of the study species.

## 4.3 MATERIALS AND METHODS

The study species, area and sites, and the experimental layout have been described in chapter 3, and more details are available in Young *et al.* (1997). In the following section, sampling procedures and statistical analysis used in this chapter are presented.

### 4.3.1 Overstorey density and species composition

The density of the overstorey species was estimated by use of belt transects (50m long by 5m wide) in each of the treatments in September 1995 when the fences were being erected. The sampling was stratified, with nine belt-transects running along a north-south axis from the nine centre posts (Fig 3.3) in each treatment. All species within the belt transects were recorded and their respective heights measured to the nearest 1.0 cm using a calibrated 2,500 cm ranging rod. Density (trees per hectare) was calculated for *A. drepanolobium* and the other woody species. *Acacia drepanolobium* heights were analysed to determine suitable tree height classes for subsequent investigations and separated into the following categories; i) < 0.49m, ii) 0.5-1.49m, iii) 1.5-2.99m and, iv) ≥ 3.0m.

### 4.3.2 Dung density counts

Dung density was estimated once in October 1997 to find out 1) whether the fences were effective in discriminating against the different herbivore categories and 2) to obtain an indication of the herbivore species presence and the relative density of each species across treatments. In each plot, nine 50 by 5 m belt transects were laid in a stratified sample. Herbivore species responsible for dung deposits encountered were identified and the number of pellets or pats counted. The sampling was initially done in the total exclusion, and then in the cattle treatment in order to be familiar with the difference between old and new dung. Only dung that was subjectively judged as reasonably fresh (at most 4-5 weeks old) was included in the dung counts.

### 4.3.3 Levels of herbivory

Five tagged twigs per tree were monitored for the presence or absence of utilization by herbivores. In each of the 18 plots, 30 trees were randomly selected for this observation (Section 4.2.4). Once a twig was utilized, the tag was removed and replaced with another randomly selected twig and tagged using the same number label. However, the tag was left if the tree had only five twigs available, i.e. all twigs had already been tagged.

Both mammalian and insect herbivores feed on *A. drepanolobium,* especially on the new growth and leaves on the twigs. Browsing by wildlife and mega-herbivores is usually evident by a break on the twig, a large area of the twig missing leaves, or presence of their footprints and spoor. Insect herbivory does not usually show signs of breakage in the twigs and only a few leaflets would be missing on a leaf. Only twigs that could reasonably be ascertained as having been browsed by mammalian herbivores were recorded.

In addition, a once-off survey was done around glades within and adjoining the KLEE experiment to evaluate the utilization of trees and shrubs. During this survey, 970 shoots of seven browse species (*Acacia nilotica, A. drepanolobium, Cadaba farinosa, Rhus natalensis, Lycium europaeum, Grewia* sp. and *Boscia* sp.) were observed for signs of browsing by herbivores between March 1996 and August 1996. For each tree or shrub on the edge of each glade, the heights were measured, and five randomly selected twigs were examined for signs of herbivore utilization. This exercise was done to assess the level of browse utilization on the edges of nutrient rich glades (Young *et al*. 1995).

During the duration of the study, 100 cattle were brought into the four hectare treatments with cattle combinations (MWC, WC, and C) for two hours once every 60 days (on two to three grazing visits a year depending on the ranch manager’s grazing plan. Each visit lasted three consecutive days of grazing for two hours each. In subsequent years, cattle were grazed in their designated plots at least once every two months, as directed by the ranch management. All grazing visits lasted two hours. The herds averaged 100 head of cattle. Whenever cattle were brought in, other herbivores (e.g. zebra, Grant's gazelle and giraffe) would move away. The presence of researchers also elicited similar response among the herbivores.

### 4.3.4 Monitoring growth and mortality

One hundred *A. drepanolobium* trees, 25 from each of the four height classes, were randomly selected and tagged with numbered aluminium tags in each plot. Each treatment had 300 tagged trees, with a total of 1,800 tagged *A. drepanolobium* trees in the six treatments. The tagged trees were measured for height and diameter at 25 cm from the ground (using a dial calliper) at the following times: March 1996; January 1997; September 1997; and February 1998. These trees were also scored for survival (dead or alive) and the resident ant species. A final check was done in September 1999 to confirm the number of the dead trees. A tree was classified as dead when it had dried up or was uprooted, and no signs of coppicing were visible. The roots of smaller trees suspected to be dead were examined to ascertain whether they were dry and dead and for signs of coppicing. Presence of flowering or fruit production was also checked and scored during each sampling occasion. Scoring was based on an estimate of the percentage of canopy (each quadrant) that was under flower or fruit.

Sub-samples of 30 trees from the 100 tagged trees in each plot were selected randomly for more detailed monitoring as it was not feasible to undertake detailed measurements of 1800 trees within a reasonable period of time. The sub-samples were 10 from each of the first three height classes (< 50 cm, > 50 < 149, >149 < 300 cm). These were monitored in March 1996, June 1996, January 1997, May 1997, September 1997, February 1998, May 1998, and September 1998. Trees over 300 cm were excluded from this survey because their inclusion would have necessitated the use of ladders, and taken up much more time. Most of the trees in the study site averaged only 150 cm, and were well covered in the sample taken.

For each of these 540 trees, the following measurements were taken:

i) height; ii) stem diameter at 25 cm from the ground; iii) crown diameter (longest axis and that perpendicular to it); iv) canopy height (distance between the top and bottom of the canopy); and v) the resident ant species were recorded.

### 4.3.5 Tree architecture and spinescence

Five branches or twigs (for smaller trees less 0.5 m in height) were selected without any known bias from the canopy (at least one from each quadrant of the canopy), and tagged with numbered aluminium tags. One branch on each tree was randomly chosen (tag # 1 was randomly selected for the first tree and this number was used for all the other trees). When a tagged twig either died or was eaten, or the tag went missing, the next lowest number was picked. The following measurements were taken from the selected twig:

i) height from the ground (from September 1997); and ii) length of the branch (or part of it if the branch was very long). The length of the latter was used to estimate the a) density of terminal twigs, b) density of terminal twigs with new growth points, c) length of new growth on that twig, d) density of swollen thorns, e) density of spines (done in March 1996, June 1996, May 1997, and May 1998), f) the length of the most distal spine (longest spine was measured), and the length of the spine most proximate to the second swollen thorn were measured in March 1996, June 1996, and May 1998.

These positions for measuring spine lengths were chosen because it was assumed that these were the most browsed sections of twig or branch.

In addition, spines were measured for trees *of A. etbaica, A. nilotica* and *A. gerardii* from branches 150 cm above the ground for comparison. Spine lengths were measured from 20 randomly selected trees of each of these species.

### 4.3.6 Seedling recruitment and survival

Seedlings of *A. drepanolobium* were sought for in the KLEE experiment. Four contiguous 1 m$^2$ plots were marked around each of 5 centre posts (used for orientation and location while in the plot). Seedlings were searched for in each of the quadrats and marked with colour-coded telephone wire. The position of each seedling was recorded in a north-facing grid, and their heights taken. This survey was done in September 1997. A second survey on the same quadrats was conducted in September 1998. Since very few seedlings were found, they were not subjected to statistical analysis, but a summary of the results is given. Seedlings were identified by the softness of their stem tissue.

### 4.3.7 Data analysis

The data was analysed using JMP-IN (Sall & Lehmi 1999) for treatment differences, contrasts and regression analysis.

a) Species composition and tree density

Differences in tree densities among treatments were analysed with one- way ANOVA (Steel & Torrie 1980). The relationship between tree diameters and height was established with linear correlation and regression.

b) Herbivory

Mean percent herbivory was calculated for each of the six treatments based on the number of twigs that had been browsed (from 540 trees). Because cattle do not eat *A. drepanolobium*, the data from the Cattle and total exclusion were therefore combined and analysed by one-way ANOVA using linear contrasts to determine the effects of the different herbivores for each sampling period. The trees sampled were further grouped into three height classes of < 100 cm, 100-200 cm, and > 200 cm after Exploratory Data Analysis (EDA). These height classes were used to analyse for differences in utilization among the tree heights using a nested design in one-way ANOVA. Differences in the incidence of herbivory of browse species from the glades were analysed using Pearson's chi-square.

c) Growth and mortality

Growth data were analysed separately for the two data sets of 1800 and 540 trees. Mean growth in height and diameter of *A. drepanolobium* were calculated between the initial measurements and the different periods of sampling. Relative growth rates (RGR) were calculated for the data set of 1800 trees. Both mean crude growth and mean RGR were analysed by one-way ANOVA for differences among the treatments. Linear contrasts were also done to determine the effects of the different herbivores on growth, and the following questions were explored.

> 1). How are wildlife and mega-herbivores different from Cattle? 2). Does the presence of mega-herbivores have any effect? 3). What is the effect of including cattle? 4). What happens in the absence of herbivory? 5.) How does wildlife (excluding mega-herbivores) differ from cattle? 6). How do treatments with herbivores differ from those without any?

Mean percent mortality was calculated for each treatment and analysed by one-way ANOVA. Linear contrasts were done to determine the effects of the different herbivores. In addition, logistic regression analysis was used to determine if there was a relationship between mortality and tree height.

### d) Tree architecture and spinescence

The six treatments were re-grouped into three categories; treatments with mega-herbivores, those with wildlife but without mega-herbivores, and those without any wildlife or mega-herbivores. Cattle do not browse on *A. drepanolobium*, therefore the responses in the cattle and total exclusion treatments were expected to be similar. The data was further categorised into three height classes, (<50cm, 50-150 cm, and >150 cm), which represent the highest possible height from which the spines were sampled. These data were analysed by one-way ANOVA for treatment differences, and Tukey-Kramer's HSD test used to compare means. Spine density data were transformed to natural logarithms and analysed by one-way ANOVA.

The relationship between the initial height or diameter of trees and the various variables measured were subjected to regression analysis. However, the relationships were weak owing to the large variations in the measured variables.

All means are given with the standard error of the mean (S.E.), unless otherwise stated.

## 4.4 RESULTS

### 4.4.1 Overstorey composition and density

The mean density of trees or shrubs was 2,323 individuals ha$^{-1}$ prior to treatments being established. Analysis of variance detected no significant block (F=0.58, P=0.71) or treatment (F=1.4, P=0.24) differences in overstorey density. The range in density among the three blocks was relatively even (Table 4.1) in support of the selection of the sites as being more or less homogenous despite the large area (72 ha). Density showed a slight increase from North to South, but the number of species recorded declined in this direction (although the tests showed no significant differences).

*Acacia drepanolobium,* at a mean density of 2,292 trees ha$^{-1}$, comprised 95% - 99% of the overstorey density. The size distribution of *A. drepanolobium* (Fig. 4.1) indicated a healthy population with young to mature trees although clumping of height classes was visible. Height distribution was similar among the blocks and the treatments. However, seedlings of *A. drepanolobium* were not recorded within the density estimation transects, suggesting that rates of recruitment and mortality were not constant (but a few seedlings were found among the grasses only after a thorough search). *Acacia drepanolobium* heights ranged from 5 to 850 cm, with a mean of 135.0 ± 0.01 cm (S.E).

The mean height of *A. drepanolobium* recorded in this study of 135 cm was almost three times lower than the mean of 350 cm reported by Coe & Beentje (1991) and Beentje (1994) although they did not specify the locations surveyed. In this study, heights of up to 1,200 cm were not uncommon in nearby ranches (Mogwooni and Ol Jogi).

Distribution of the other woody species was similar across the treatments, though the North block had a significantly higher density of non-*A. drepanolobium* species (F=4.3, P=0.018) compared with the other blocks. Trees and shrubs less than 100 cm in height comprised almost 60% of the density of this group of species.

Table 4.1 Mean density (individuals ha$^{-1}$ ± S. E) and frequency (%) of woody species in each block of the KLEE experiment. Estimates were made in September 1995

| | NORTH | | CENTRAL | | SOUTH | |
|---|---|---|---|---|---|---|
| Species | Density | Frequency | Density | Frequency | Density | Frequency |
| *A. drepanolobium* | 1,959 ± 357.0 | 98.2 | 2,235 ± 250.0 | 95.5 | 2,616 ± 280.0 | 99.0 |
| *A. mellifera* | 11 ± 4.2 | 0.4 | 9 ± 5.5 | 0.5 | 4 ± 1.7 | 0.1 |
| *A. brevispica* | 1 ± 1.2 | 0.1 | 3 ± 2.5 | 0.1 | 3 ± 2.5 | 0.0 |
| *A. seyal* | 1 ± 1.2 | 0.0 | - | 0.1 | - | 0.0 |
| *Cadaba farinosa* | 38 ± 10.9 | 0.8 | 19 ± 3.7 | 1.9 | 5 ± 2.5 | 0.2 |
| *Lycium europaeum* | 9 ± 5.5 | 0.1 | 3 ± 2.5 | 0.4 | 9 ± 4.4 | 0.3 |
| *Balanites aegyptiaca* | 3 ± 2.5 | 0.1 | 1 ± 1.2 | 0.1 | - | 0.0 |
| *Boscia coriandale* | - | 0.1 | 1 ± 1.2 | 0.0 | 3 ± 2.5 | 0.1 |
| *Grewia sp.* | 7 ± 4.7 | 0.1 | 3 ± 2.5 | 0.4 | 1 ± 1.2 | 0.0 |
| *Rhus natalensis* | 6 ± 4.0 | 0.2 | 4 ± 2.5 | 0.3 | 4 ± 1.7 | 0.0 |
| *Carissa edulis* | 1 ± 1.2 | 0.0 | - | 0.1 | - | 0.1 |
| All species | 2,037 ± 375.0 | | 2,276 ± 249.0 | | 2,647 ± 275.0 | |

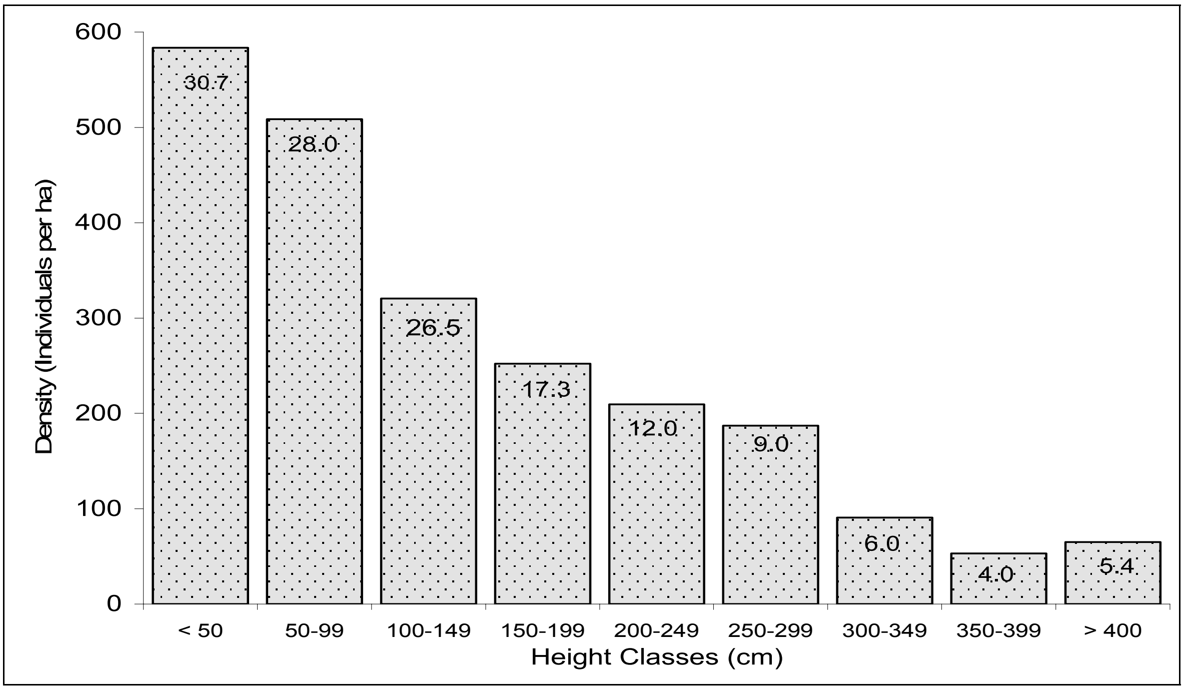

Fig. 4.1 Height class distribution of *A. drepanolobium* density sampled within the KLEE experiment. The distribution shows a clustered reverse J-shape. Standard errors are inset. N = 5517. Total area surveyed, 24 300m$^2$.

### 4.4.2 Relationship between tree height and stem diameter

The relationship between tree height and stem diameter at 25 cm from the ground was very strong, with over 97% of the variance accounted for (Fig. 4.2), though the standard error was high (18%). There were a few outliers, which are expected in the range given that some trees are either stunted by the effects of herbivory, or because the shape of the tree trunk is not entirely cylindrical. Nonetheless, height can be predicted by measuring the stem diameters using the equation Y = 0.52x + 0.0585, adjusted $R^2 = 0.97$.

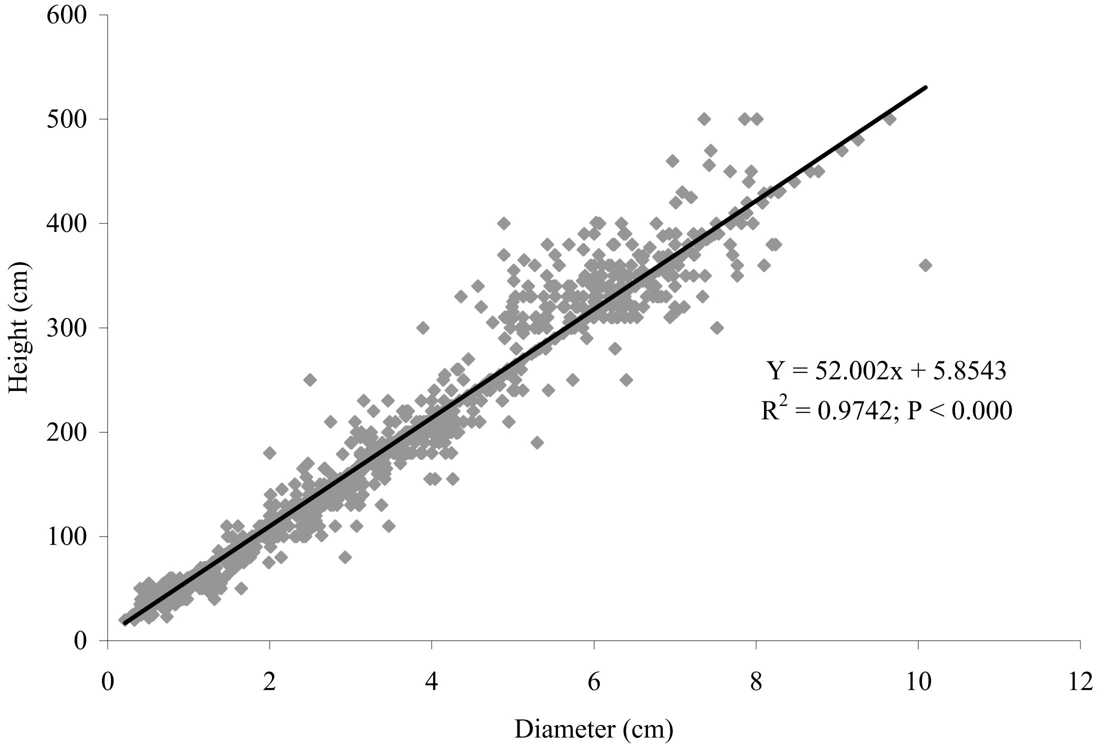

Fig. 4.2 Relationship between stem diameter and height of *A. drepanolobium*. Predictive equation is inset.

### 4.4.3 Herbivore presence and dung density counts

Herbivores that frequent this ecosystem have been documented by Young *et al.* (1998), and are also given in the wildlife counts (chapter 3, Table 3.1). The dung survey conducted in the KLEE experiment showed only 12 herbivore species as opposed to the 16 recorded by Young *et al.* (1998). Zebras had the greatest dung density in all treatments to which wildlife had access (Table 4.2). The species whose dung was positively identified were elephant, giraffe, Grant's gazelle, steenbok, cattle, zebra, eland, hartebeest, hare, bushbuck and buffalo.

Table 4.2 Summary of mean herbivore dung density (pats/piles) per hectare in five herbivore treatments (mega-herbivore, wildlife and cattle – MWC, mega-herbivore and wildlife – MW, wildlife and cattle – WC, wildlife – W, and Cattle - C) of the KLEE project in August 1996

| Treatment | Elephant | Giraffe | Grant's gazelle | Steenbok | Cattle | Zebra | Others |
|---|---|---|---|---|---|---|---|
| MWC | 44.4 | 22.2 | 111.1 | 57.8 | 133.3 | 275.6 | 84.0 |
| MW | 71.1 | 35.6 | 62.2 | 17.8 | 0.0 | 293.3 | 62.2 |
| WC | 4.4 | 8.9 | 71.1 | 48.9 | 151.1 | 257.8 | 49.0 |
| W | 4.4 | 13.3 | 48.9 | 35.6 | 0.0 | 240.0 | 44.0 |
| C | 0.0 | 0.0 | 0.0 | 13.3 | 155.6 | 0.0 | 40.0 |

The cattle treatment successfully excluded all herbivores except steenbok and hare, indicating that some browsing, especially of shorter trees, could have taken place in the cattle and total exclusion treatments. The mega-herbivore and wildlife treatments had the greatest presence of herbivore dung. Grant's gazelles were probably the most important browsers in the treatments because of their great dung density, and also because they were the most often seen browsers in the KLEE experiment. The dung density results indicate grazing and browsing pressure was probably low. Impala, though common in Laikipia plateau, were conspicuously absent in the black-cotton ecosystem.

### 4.4.4 Herbivory of shoots

#### *4.4.4.1 Utilization of trees and shrubs within and around glades*

The browse species, *Acacia nilotica, A. drepanolobium, Cadaba farinosa, Rhus natalensis, Lycium europaeum, Grewia* sp. and *Boscia* sp. differed in the number of available shoots eaten (Pearson chi-square 123.4, P=0.0002). *Cadaba farinosa* was the most utilized (80%) and *A. drepanolobium* the least (9.1%), (Fig. 4. 3), indicating that the other woody species were generally preferred to *A. drepanolobium* despite the latter's dominance in the ecosystem.

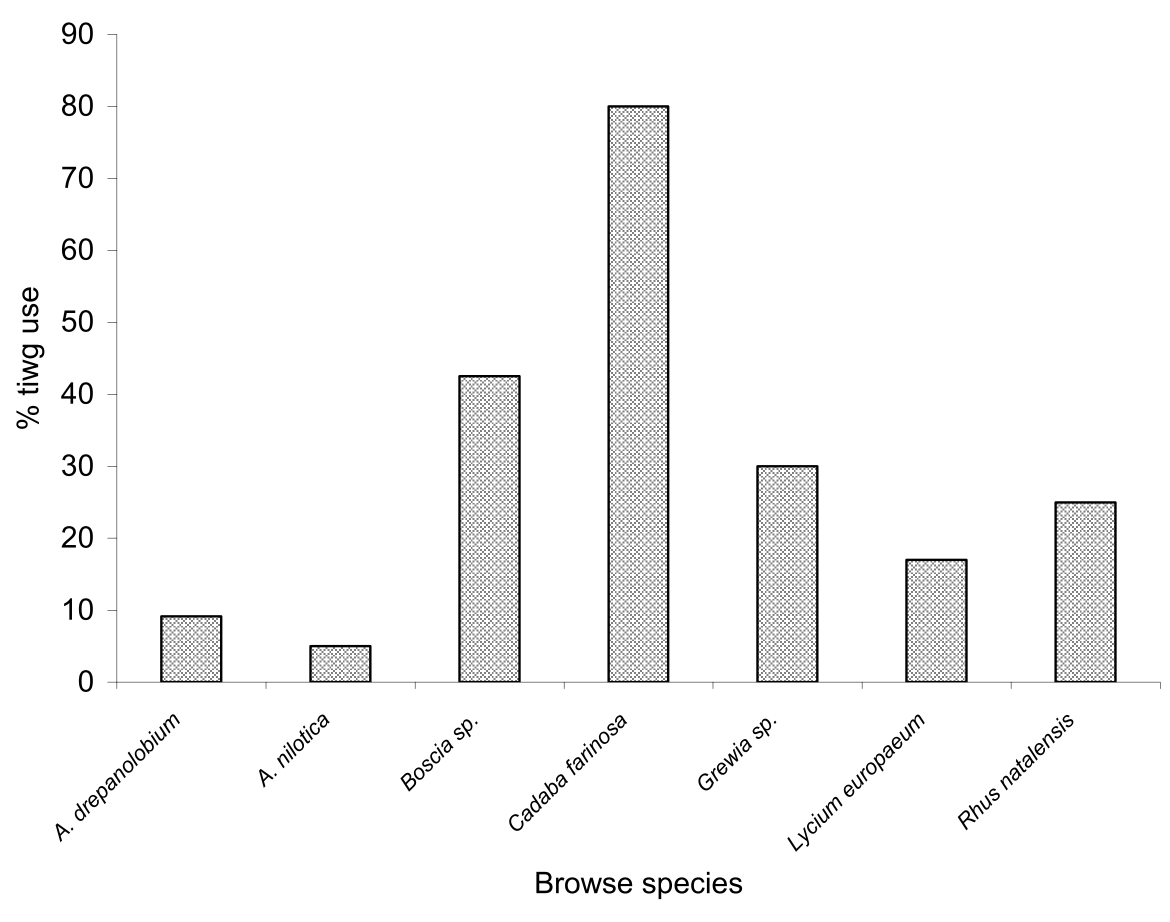

Fig. 4.3 Mean percent utilization of twigs for different browse species by herbivores in glades within and around KLEE between March and August 1996.

Trees shorter than 50 cm were eaten the most compared with taller ones within the glades (Fig. 4.4). The < 50 cm height class was also the most abundant.

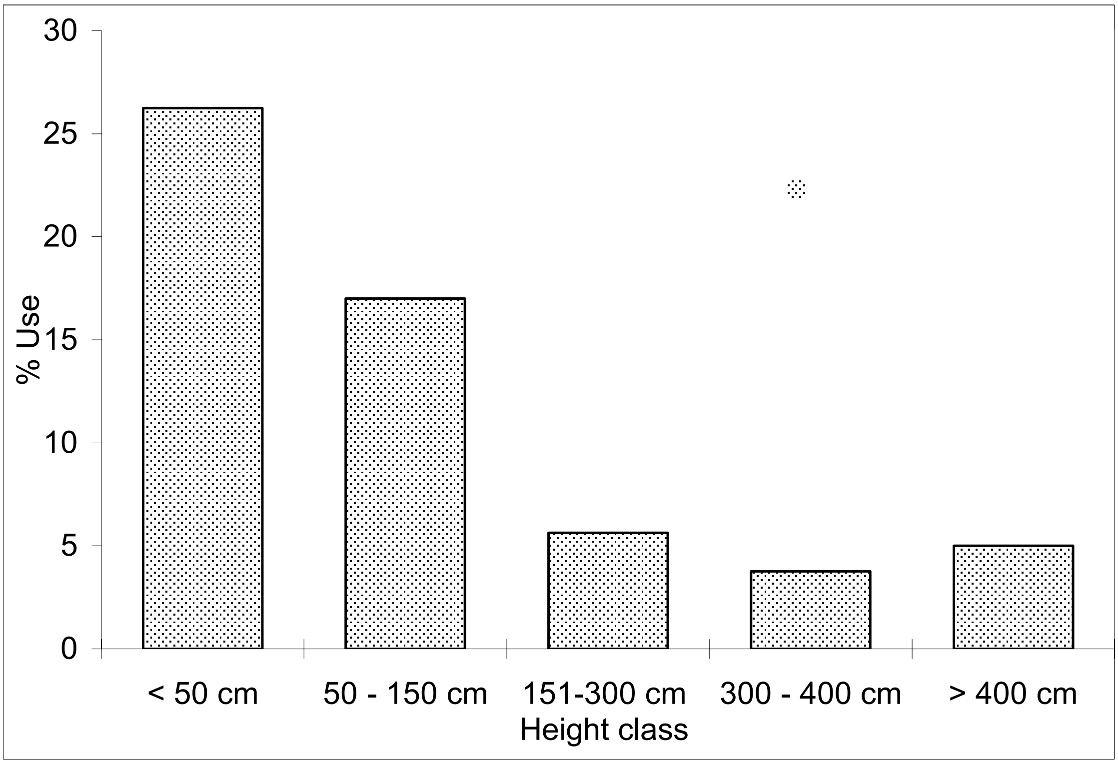

Fig. 4.4 Mean percent utilization of *A. drepanolobium* twigs by height class around glades May to August 1996.

#### *4.4.4.2 Utilization of Acacia drepanolobium among the treatments*

Utilization of *A. drepanolobium* twigs by herbivores in the experimental exclosures was very low during the study period (Fig. 4.5). The number of twigs utilized was converted to percent use per tree. Herbivores seen browsing *A. drepanolobium* trees were eland, giraffe, Grant's gazelle, elephant, hartebeest, goat and camel. Baboons and Patas monkeys were also seen eating the leaves and breaking open the galls of *A. drepanolobium*. These primates ate the young reddish-green galls as well as the "brood of the ants" in the mature galls.

The proportion of trees browsed was similar in the North, Central and South blocks (28.0, 25.0, and 23.3 % respectively) suggesting an even distribution of browsers within the large experimental site. However, the percent use of twigs was significantly different in the three blocks (F=4.6, P=0.01), with the South block (6%) being significantly lower than either North or Central blocks (7.2% and 7.1%) respectively.

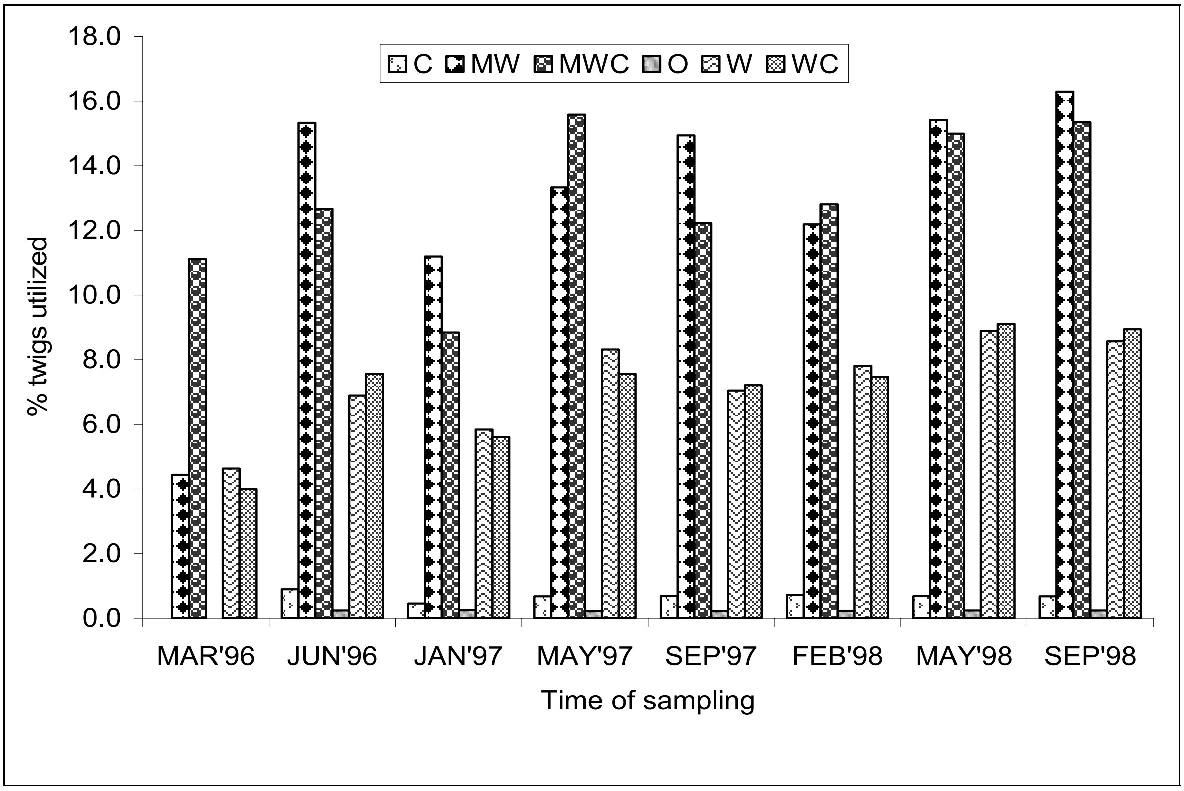

Fig. 4.5 Mean percent utilization of *A. drepanolobium* twigs over time under different herbivore treatments. C-Cattle; MWC-mega-herbivores, wildlife & cattle; MW-mega-herbivores & wildlife; O-Total exclusion; W-wildlife.

The proportion of trees browsed over the study period was greater in treatments with wildlife or mega-herbivores than those without them (Table 4. 3). The trees were regrouped into three new height-classes of i) < 100 cm, ii) 101-200 cm, and iii) > 200 cm after the initial exploratory data analysis (E D A) indicated distinct patterns based on these height classes.

Table 4.3 Number of *A. drepanolobium* trees browsed in three height classes among herbivore treatments. Amounts in (parenthesis) indicate the percent of numbers browsed with respect to the observations. Dead and lost trees were not included, and the data was pooled for all the observations made between March 1996 and September 1998. N = 4164

| Height class (m) | MW | MWC | W | WC | C | O |
|---|---|---|---|---|---|---|
| < 100 | 99 (38.1) | 131 (42.5) | 50 (18.4) | 70 (25.5) | 14 (5.0) | 7 (2.7) |
| 101-200 | 166 (56.1) | 109 (44.9) | 105 (37.5) | 83 (28.4) | 0 (0.0) | 0 (0.0) |
| > 200 | 63 (47.0) | 74 (44.4) | 40 (27.2) | 35 (29.1) | 0 (0.0) | 0 (0.0) |
| Total | 328 (47.5) | 314 (44.4) | 195 (27.9) | 188 (27.5) | 14 (2.0) | 7 (1.0) |

Similarly, E D A showed that utilization of *A. drepanolobium* twigs had three distinct patterns based on the treatments; treatments with mega-herbivores, (mega-herbivores with wildlife and cattle), wildlife minus mega-herbivores (wildlife, and wildlife with cattle), and those without any wildlife or mega-herbivores (cattle and total exclusion).

Use of twigs was greatest in treatments with mega-herbivores, whilst wildlife treatments recorded moderate use levels (Fig 4. 5). Linear contrasts showed that mega-herbivores contributed significantly to twig utilization (F=499.99, P<0.0001). Wildlife treatments also had significantly more browsed twigs than either cattle or total exclusion treatment. All the twigs browsed in the cattle and total exclusion treatments were less than 100 cm from the ground (Table 4.3), and the percentage of browsed twigs did not exceed 1% and 0.5% respectively, indicating the effectiveness of the electric fences in keeping out large herbivores. This observation also confirms that cattle do not browse on *A. drepanolobium*.

Herbivory recorded in the cattle and total exclusion treatments can be attributed to browsing by steenbok and hare, which could easily pass through the strands of the electric wires (see section 4.3.3). Baboons and Patas monkeys were also seen inside these plots eating on *A. drepanolobium* trees. In many cases, these primates chewed away the tags on the twigs. Among the treatments with wildlife or mega-herbivores, all tree size classes were evenly used, although elephants were at times destructive.

Utilization in 1998 was greater than in 1997, which in turn, was greater than in 1996. On a seasonal basis, May-June periods recorded similar levels of twig utilization. September also showed similarity in the proportion of twigs used. Twig use was greatest towards the end of the data collection period (September 1998) compared with the start (March 1996). This may be due to the animals becoming accustomed to the presence of the electric fence and disturbance by the researchers visiting the KLEE project. Twig utilization was generally low, with the highest recorded mean being 16.3% in the mega herbivore and wildlife treatment in September 1998.

The relationship between percent twig use and height of tree showed a lot of variation, the relationship was weak, and initial height accounted for less than 10% of the observed variance (Fig. 4.6). This suggests that the browsers either did not choose specific heights to browse, or there were a variety of browsers that could browse at different heights. The data in Table 3.1 confirms that there were a variety of browsers that could browse at different heights. For example, Grant's gazelle is expected to browse at lower heights than eland or giraffe, while steenbok are expected to browse at heights that are lower than a Grant's gazelle.

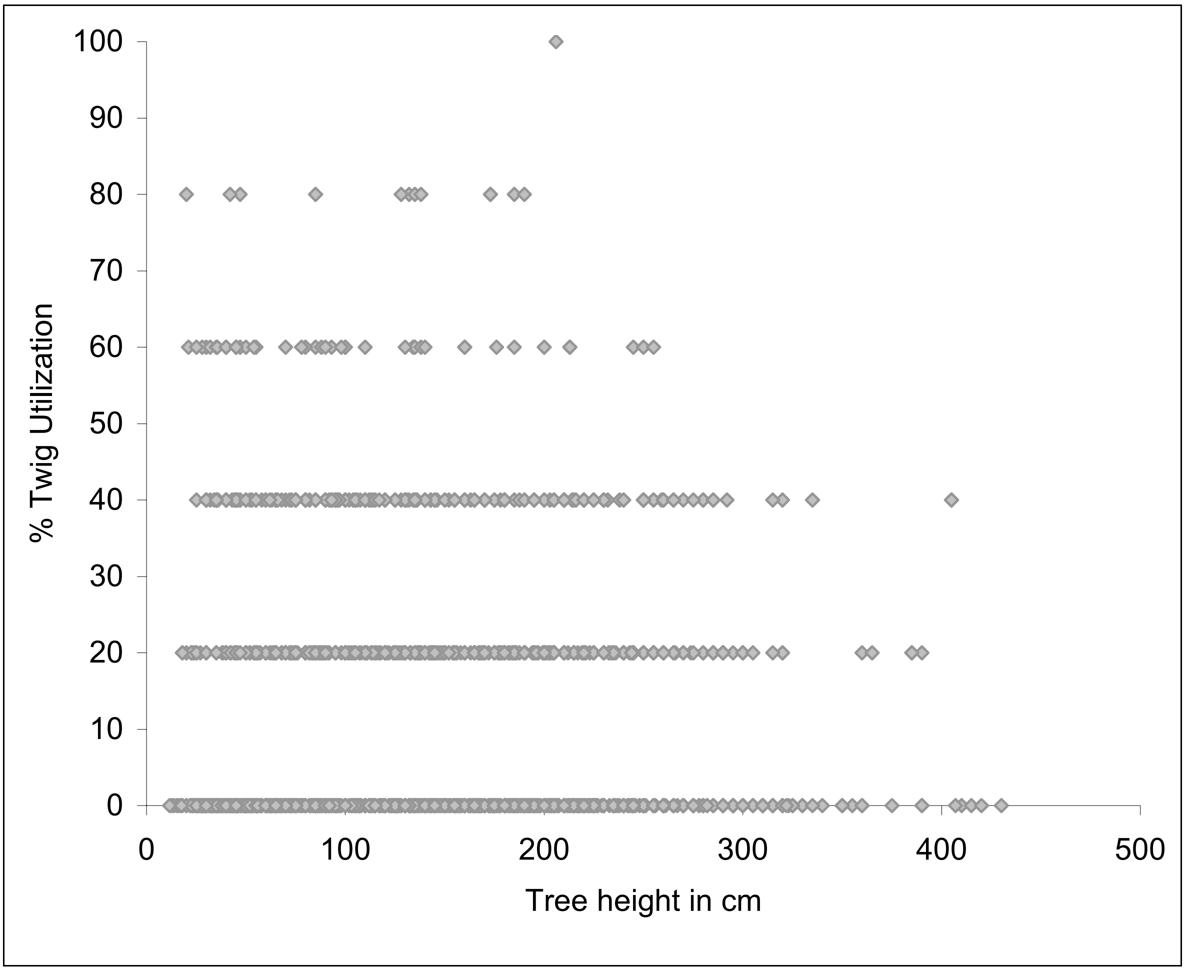

Fig. 4.6 Relationship between mean percent twig utilization and height of *A. drepanolobium* trees.

It is, however, evident that twig utilization of larger trees was less than that of smaller trees when the envelope of the tallest tree height for any given level of twig use is examined (Fig. 4.6).

### 4.4.5 Growth of *Acacia drepanolobium*

#### *4.4.5.1* ***Case of 1800 tagged trees***

*Acacia drepanolobium* trees grew in height by a mean of 47.6 ± 1.05 cm (S.E.) over the 23 month experimental period (March 1996 to February 1998 inclusive), or a mean of 24.9 cm yr$^{-1}$. With a mean annual rainfall of 742.7 mm recorded during the study period, which translates to 3.35 cm per 100 mm of rainfall (Table 4.4). Growth in height during the sampling period was different (F=6.74, P<0.0001) among the treatments, and was greatest in the cattle treatment and least in the wildlife and cattle treatment (WC).

Table 4.4 Mean growth in height (cm) (± S.E) of *A. drepanolobium* among six herbivore treatments, mega-herbivore, wildlife and cattle - (MWC), mega-herbivore and wildlife - (MW), wildlife - (W), wildlife and cattle - (WC), cattle - (C), and total exclusion - (O), during three sampling periods, and the Relative Growth Rate (RGR) cm $cm^{-1}$ $yr^{-1}$ over the entire growth period. Cumulative rainfall for each period is in the last row

| Treatment | Mar 96 - Jan 97 | Jan 97 - Sep 97 | Sep 97 - Feb 98 | Mar 96 – Feb 98 | RGR Mar 96 - Feb 98 Cm $cm^{-1}$ $yr^{-1}$ |
|---|---|---|---|---|---|
| MWC | $19.5 \pm 0.73^{a}$ | $17.1 \pm 0.90^{a}$ | $11.1 \pm 1.50^{b}$ | $49.1 \pm 2.22^{bd}$ | $17.5 \times 10^{-3} \pm 0.0^{ab}$ |
| MW | $18.9 \pm 0.69^{a}$ | $13.8 \pm 0.86^{bc}$ | $14.3 \pm 2.05^{ab}$ | $49.2 \pm 2.78^{bd}$ | $15.4 \times 10^{-3} \pm 0.0^{bc}$ |
| W | $17.5 \pm 0.61b^{c}$ | $13.6 \pm 0.66^{b}$ | $10.4 \pm 1.93^{b}$ | $42.7 \pm 2.26^{bc}$ | $14.6 \times 10^{-3} \pm 0.0^{c}$ |
| WC | $17.0 \pm 0.60^{b}$ | $11.5 \pm 0.69^{d}$ | $11.3 \pm 1.60^{b}$ | $38.8 \pm 2.12^{c}$ | $14.9 \times 10^{-3} \pm 0.0^{bc}$ |
| C | $20.3 \pm 0.69^{a}$ | $17.0 \pm 0.84^{a}$ | $17.8 \pm 1.33^{a}$ | $56.8 \pm 2.83^{a}$ | $18.7 \times 10^{-3} \pm 0.0^{a}$ |
| O | $19.3 \pm 0.66^{a}$ | $13.3 \pm 0.73^{ac}$ | $13.6 \pm 1.70^{ab}$ | $49.7 \pm 2.37^{d}$ | $15.4 \times 10^{-3} \pm 0.0^{bc}$ |
| Rainfall (mm) | 393.9 | 504.5 | 588.2 | 1486.6 | |

Superscripts within a column indicate treatments that are different (P=0.05).

Linear contrasts revealed that the inclusion of mega-herbivores did not have any effect on growth compared with treatments without them (F=1.00, P=0.31). This was unexpected as elephants and giraffes are known to be heavy browsers of *Acacia* species, and were thus expected to constrain vertical growth. Treatments with wildlife (MWC, MW and W) generally had lower mean growth compared with those without them. In particular, wildlife treatments had significantly lower mean growth (F=17.49, P<0.001) compared with cattle treatments. Relative growth rates were also different among the treatments (F=2.86, P=0.014). Treatments with wildlife had relatively lower RGR, and linear contrasts showed significant differences between the cattle and wildlife treatments (F=9.3, P=0.002).

The relationship between initial height and growth in height was weak, with $R^2$ values of less than 5% in all treatments. In general, growth increased marginally with increase in initial height, showing a weak peak between 100 and 200 cm. The growth data showed a lot of variation and no transformation improved the relationship.

Relative growth rate decreased exponentially with increasing plant height, but RGR was highly variable for any given height (Fig 4.7). Vertical growth of *A. drepanolobium* in the wildlife treatment (W) showed a weakly different pattern to those of the other five treatments, exhibiting a weakly concave pattern, compared with the relatively convex pattern of the other treatments.

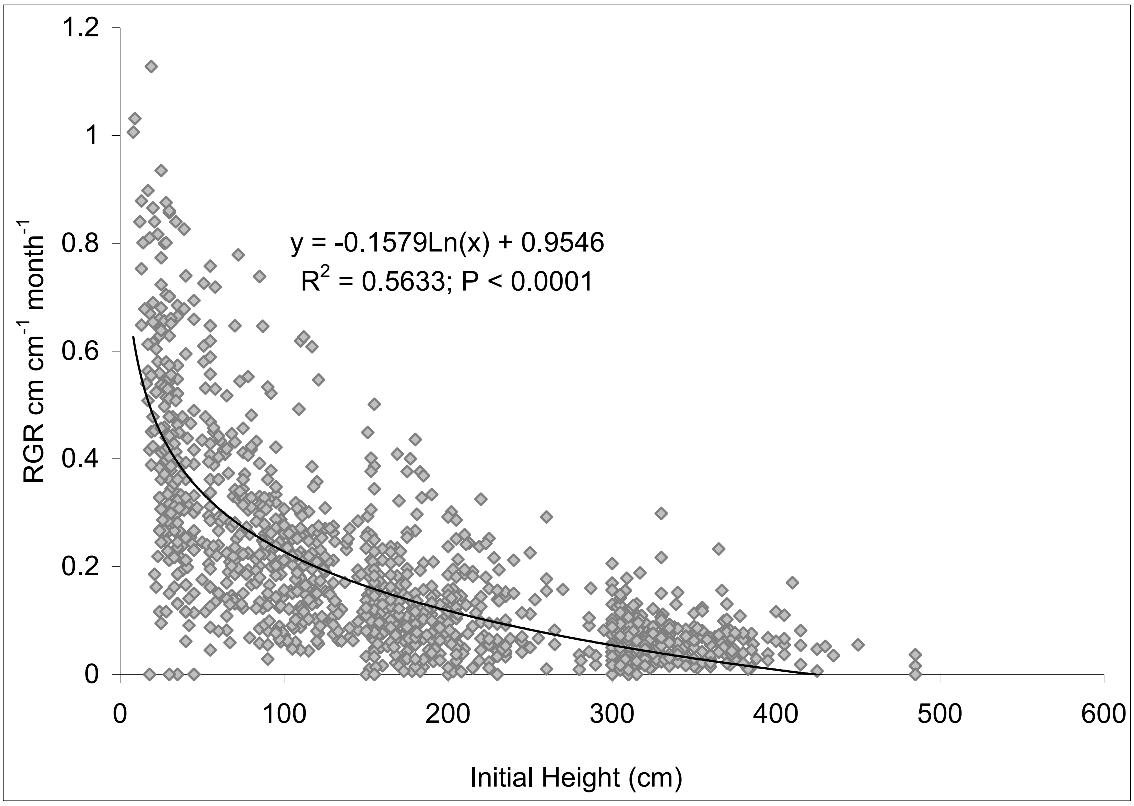

Fig. 4.7 Relationship between relative growth rate and initial height of *A. drepanolobium* March ’96 to February ’98.

Growth in height was greatest in trees of about 100 cm, and least for trees smaller than 50 cm. Taller (older) trees recorded greater growth than shorter (presumably younger) ones, though less than trees of medium height. Conversely, shorter trees had a greater RGR than taller trees (Fig. 4.7). The intercept of Fig. 4.7 indicate differences in the growth rates relative to the initial heights among the treatments. Similarly, there were differences in RGR with respect to diameter increase relative to the initial diameter (Fig. 4.8).

Mean increase in diameter ranged from 1.40 cm to 1.55 cm over the 23-month period, a mean of 0.73 cm to 0.81 cm per year. The treatment means were not different (F=0.83, P=0.53). Linear contrasts (Table 4.6) did not identify effect of any herbivore type (F=0.81, P=0.51).

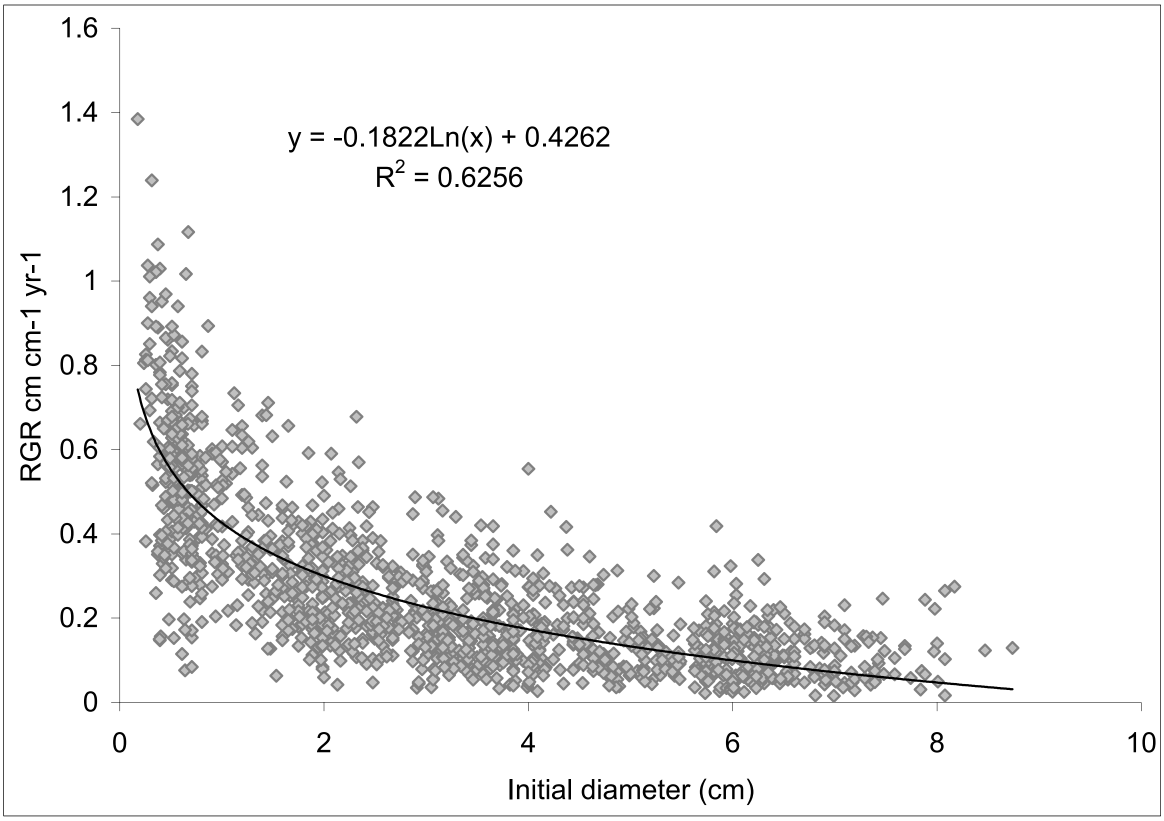

Fig. 4.8 Relationship between relative growth rate and initial stem diameter of *A. drepanolobium* March '96 to February '98.

Height class analysis of the data showed that mean growth in height was greatest (54.9 ± 1.96 cm (S.E)) in the 50-150 cm range, and least (39.76 ± 1.68 cm (S.E)) in the < 50 cm height-class. The 151-300 cm and > 300 cm height classes recorded 50.4 ± 2.15 cm (S.E) and 42.4 ± 1.84 cm (S.E) of growth respectively. Growth in height was different among the four height classes (F=4.82, P < 0.0001). Growth in diameter was also different among the height classes (F=5.83 P < 0.0001) but showed a linear trend among the four height classes, with the greatest growth (1.68 ± 0.06 cm (S.E.)) in the > 300 cm height class and least (1.08 ± 0.04 cm (S.E.)) in the < 50 cm height class. The 50-150 cm class had 1.45 ± 0.04 cm (S.E.) and the 151-300 cm class 1.56 ± 0.05 cm (S.E.) of growth.

#### 4.4.5.2 Growth of Acacia drepanolobium: Detailed analysis of 540 tagged trees

A more detailed and rigorous monitoring of a sub-sample of 540 trees showed the following:

i) Growth in height and diameter of this sub-sample closely mirrored that of the parent population (Fig. 4.9.). Relative growth rates in height were different among the treatments

(F=3.17, P=0.008), being greatest in the cattle treatment and least in wildlife and cattle treatment. Growth in diameter did not differ among the treatments (F=1.10, P =0.35). Again, the growth patterns showed a strong seasonal tendency, with growth taking place after the rains start falling. The distribution and length of the rainy period is also a factor that may contribute to the apparent lack of fit.

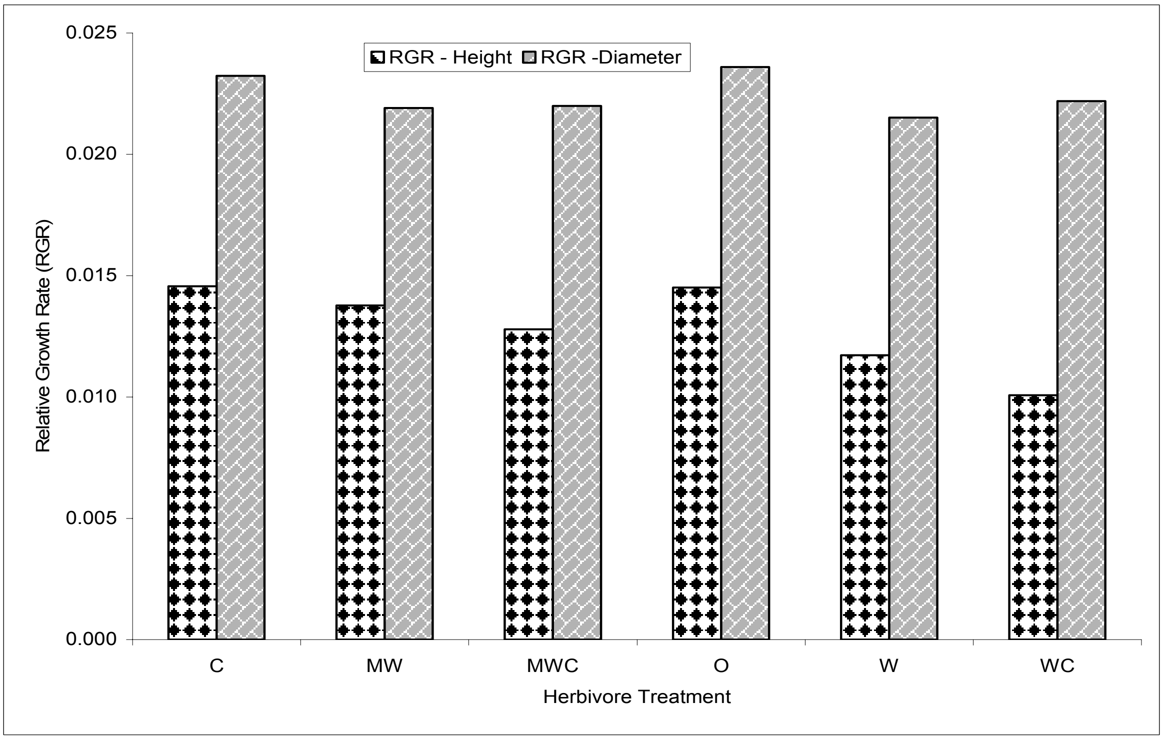

Fig. 4.9 Cumulative (March ’96 to February ’98) relative growth rate in height and stem diameter of *A. drepanolobium* among herbivore treatments for 540 tagged trees.

ii) Twigs monitored for increase in shoot length showed an overall mean increase of 6.8 cm to 9.1 cm over the study period (Fig. 4.10; Table 4.5). These increments were different among the herbivore treatments (F=5.29, P<0.001). However, a large number of trees did not register any growth in the sampled twigs, thereby lowering the mean growth recorded. The mega-herbivore and wildlife treatment had the greatest increase in shoot length, while it had been expected that persistent browsing by these herbivores would stifle any increase in shoot length. Linear contrasts indicate that cattle treatments (C) had significantly greater increases in shoot length compared with wildlife only treatments. The presence or absence of herbivores did not affect increase in shoot length.

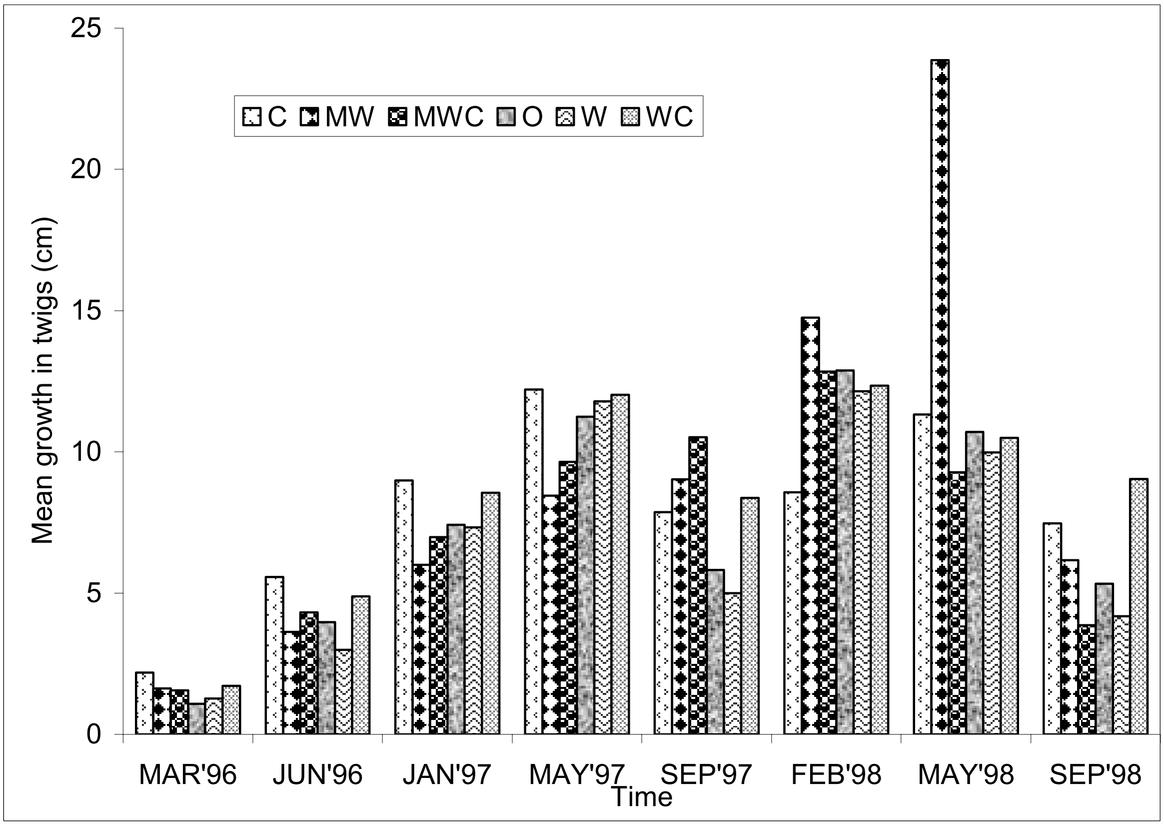

Fig. 4.10 Mean growth in twigs of *A. drepanolobium* trees on different herbivore treatments over time.

iii) The number of new shoots growing on a unit length of a twig did not differ among the treatments, averaging four new growing shoots per meter of twig length, suggesting that herbivore type did not influence production of new shoots. However, the total number of shoots per meter of twig length differed among the treatments (F=12.2, P<0.000), evidence that the different herbivore types probably had different effects on the longevity of the twigs/shoots. Shoot density fluctuated with time, though a general decrease over time was observed (Fig. 4.11).

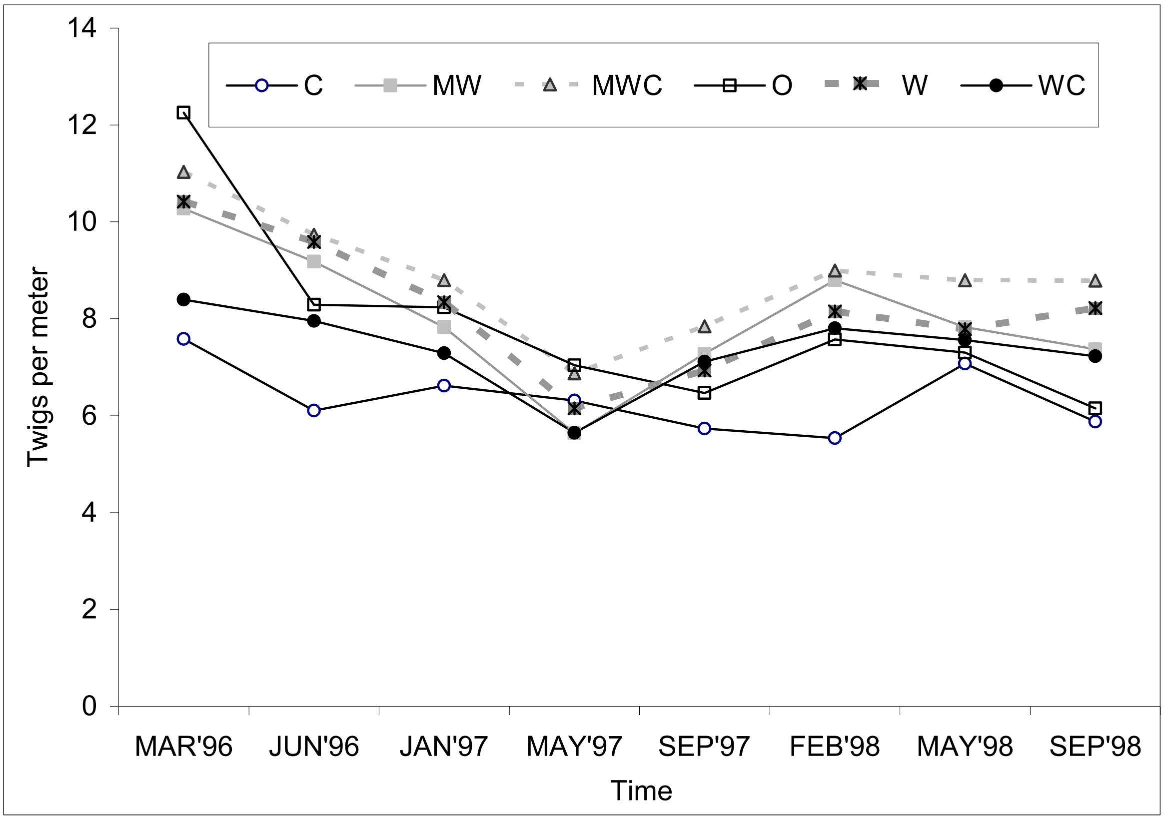

Fig. 4.11 Mean density of shoots per meter of twig length for *A. drepanolobium* trees among herbivore treatments over time.

Some of these results were confounding (Table 4.5). Treatments with known browsers (mega-herbivores, wildlife and cattle; mega-herbivores and wildlife; and wildlife only) had a significantly greater density of shoots than those without (cattle and total exclusion) (F=19.9, P<0.0001), whilst the cattle treatment had significantly lower (F=21.9, P<0.0001) shoot density than the total exclusion of herbivores, yet the last two treatments were expected to be the same, because cattle do not feed on *A. drepanolobium* trees and was, therefore, a similar treatment to total exclusion of herbivores.

Table 4.5 Mean density of new shoots, total shoots, spines per meter of twig or branch, and growth of *A. drepanolobium* twigs among different herbivore combinations between March 1996 and September 1998. See Table 4.3 for the key to treatment abbreviations

| Attribute / Treatment | Density of new shoots | Density of all shoots | Density of spines (pairs) | Density of galls | Twig growth (cm) |
|---|---|---|---|---|---|
| MWC | $3.8 \pm 0.14$ | $8.9 \pm 0.24^{a}$ | $91.7 \pm 1.79^{a}$ | $7.2 \pm 0.15^{b}$ | $7.4 \pm 0.35^{bc}$ |
| MW | $3.8 \pm 0.16$ | $8.1 \pm 0.26^{b}$ | $84.5 \pm 1.81^{bc}$ | $7.7 \pm 0.20^{a}$ | $9.1 \pm 0.45^{a}$ |
| WC | $3.7 \pm 0.12$ | $7.4 \pm 0.23^{c}$ | $86.9 \pm 1.82^{ab}$ | $6.9 \pm 0.14^{bc}$ | $8.4 \pm 0.33^{a}$ |
| W | $3.7 \pm 0.15$ | $8.2 \pm 0.28^{b}$ | $87.2 \pm 1.82^{ab}$ | $7.1 \pm 0.14^{b}$ | $6.8 \pm 0.34^{d}$ |
| C | $3.5 \pm 0.14$ | $6.4 \pm 0.19^{d}$ | $86.2 \pm 1.79^{bc}$ | $6.6 \pm 0.13^{c}$ | $8.0 \pm 0.35^{ab}$ |
| O | $3.6 \pm 0.15$ | $8.0 \pm 0.27^{bc}$ | $81.6 \pm 1.85^{c}$ | $6.8 \pm 0.21^{bc}$ | $7.3 \pm 0.34^{bc}$ |

Figures with different superscripts within a column indicate treatments that are different (P=0.05). There were no differences in density of new shoots among the treatments.

These results indicate that factors other than herbivory (or in combination with herbivory) determine the number of shoots. The density of shoots was significantly lower in cattle than in wildlife treatments (F=28.9, P<0.0001), and treatments with mega-herbivores had significantly more (F21.8, P<0.0001) shoots than those with wildlife.

iv) Gall density was different among the treatments (F=4.86, P=0.0002). Mega-herbivore treatments had significantly greater gall densities than those without them (F=15.33, P<0.0001). However, linear contrasts did not show any effect of herbivory (F=0.57, P=0.44).

v) Canopy volume showed a definite time trend, increasing over time in all the treatments (Fig 4.12). However, some fluctuations occurred in September 1997 and February 1998 censuses in cattle, mega-herbivore and wildlife, and wildlife and cattle treatments. The increase in canopy volume indicates an increase in the bushiness of this system and suggests that the herbivore density was probably too low to maintain or suppress it.

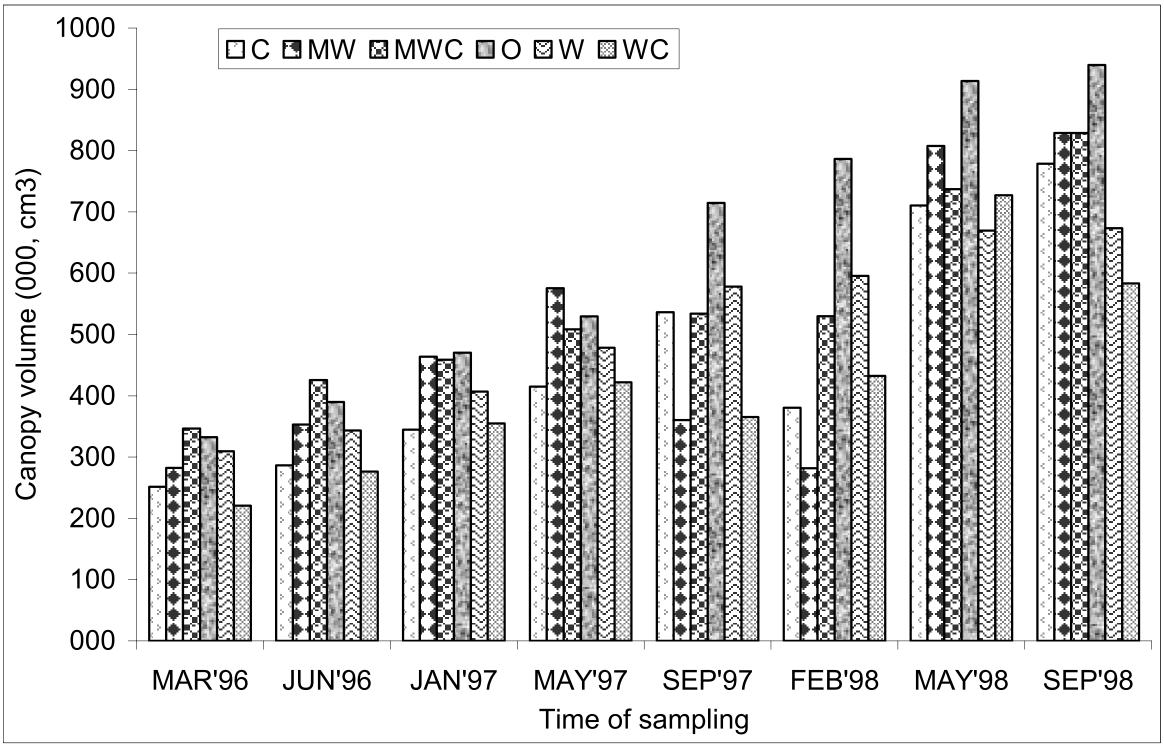

Fig. 4.12 Changes in the canopy volume of *A. drepanolobium* under different herbivore treatments over time, indicating a general increase in cover.

Table 4.6 gives a detailed summary of linear contrast analysis for the various variables presented above.

Table 4.6 Summary of linear contrast analysis (F and P values) for various *A. drepanolobium* variables. The last column indicates the ANOVA values for the whole model. See the notes below for explanation of the treatment combinations and abbreviations used

| Contrasts | O vs. Others | | O vs. C | | M vs. Others | | C vs. Others | | M + W vs. others | | C vs. W | | ANOVA tests | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Variable | F | P | F | P | F | P | F | P | F | P | F | P | F | P |
| Growth - height | 0.84 | 0.361 | 4.39 | 0.036 | 1.00 | 0.317 | 0.26 | 0.608 | 15.70 | 0.0001 | 17.45 | < 0.001 | 6.74 | 0.0001 |
| Growth - diameter | 0.06 | 0.809 | 0.48 | 0.488 | 1.08 | 0.297 | 0.35 | 0.552 | 0.21 | 0.643 | 0.88 | 0.346 | 0.83 | 0.531 |
| RGR - height | 0.58 | 0.448 | 5.91 | 0.015 | 0.38 | 0.536 | 5.63 | 0.018 | 3.11 | 0.078 | 9.31 | 0.002 | 2.86 | 0.141 |
| RGR - diameter | 0.65 | 0.419 | 0.26 | 0.607 | 0.004 | 0.944 | 4.14 | 0.042 | 0.41 | 0.521 | 0.28 | 0.596 | 1.05 | 0.385 |
| Growth - twigs | 2.89 | 0.080 | 2.07 | 0.150 | 3.68 | 0.055 | 0.45 | 0.501 | 0.91 | 0.340 | 5.20 | 0.023 | 5.29 | < 0.001 |
| New shoots | 0.68 | 0.410 | 0.04 | 0.850 | 1.66 | 0.197 | 0.02 | 0.893 | 2.40 | 0.122 | 0.80 | 0.372 | 0.56 | 0.727 |
| Shoot density | 0.63 | 0.426 | 21.90 | < 0.001 | 21.67 | < 0.001 | 7.34 | 0.007 | 19.94 | < 0.001 | 27.75 | < 0.001 | 12.23 | < 0.001 |
| Canopy volume | 26.17 | 0.000 | 20.66 | < 0.001 | 0.29 | 0.589 | 9.40 | 0.002 | 3.74 | 0.009 | 1.19 | 0.275 | 7.78 | < 0.001 |
| Gall density | 0.56 | 0.447 | 2.12 | 0.145 | 15.33 | < 0.001 | 6.86 | 0.009 | 8.99 | 0.003 | 4.38 | 0.036 | 4.86 | < 0.001 |
| Herbivory | 232.72 | 0.000 | 0.34 | 0.560 | 499.99 | 0.000 | 0.12 | 0.729 | 559.23 | 0.000 | 101.17 | 0.000 | 141.7 | 0.000 |
| Mortality | 0.21 | 0.644 | 0.12 | 0.721 | 10.31 | 0.001 | 1.06 | 0.302 | 1.36 | 0.243 | 2.04 | 0.152 | 3.42 | 0.005 |

O vs. Others. Contrast between total exclusion and all other five treatments.
O vs. C. Contrast between total exclusion and cattle only treatment.
M vs. Others. Contrast between treatments with mega-herbivores and those without.
C vs. Others. Contrast between treatments with cattle and those without cattle.
M+W vs. Others. Contrast between treatments with mega-herbivores and wildlife and those without any wildlife
C vs. W. Contrast between the cattle and wildlife treatments only.
Figures in bold indicate differences (P ≤ 0.05).

As expected, the total exclusion treatment showed the greatest mean canopy volume. The mega-herbivore, cattle, and wildlife (MWC) had low means while the cattle (C) treatment had high mean values. These observations are consistent with the twig growth data reported in section 4.3.5. Linear contrasts showed that herbivores significantly stifled any increase in the canopy cover (F=2.7, P=0.02), and that wildlife treatments had a greater effect on canopy volume than did mega-herbivore treatments (F=5.2, P= 0.02). Therefore, the presence of wildlife suppressed any increase in canopy volume, while the effect of mega-herbivores was less. No other contrasts were significant (Table 4.6). This observation was probably due to the greater number of wildlife that visited the experimental site compared with the mega-herbivores, which were fewer in number. For instance, a herd of Grant's gazelle was resident within the KLEE plots, while mega-herbivores only visited on transit to other grazing areas.

vi) Spine density and spine length

The mega-herbivore, wildlife and cattle treatment (MWC) had the greatest, while mega-herbivore and wildlife treatment had, surprisingly, the least mean spine density per meter of twig length (Table 4.7). Spine density was different among the treatments (F=2.47, P=0.031). Tukey-Kramer's HSD test showed that the mega-herbivore, wildlife and cattle treatment (MWC) was more spinescent than the total exclusion treatment at P=0.05. The density of spines showed an overall but marginal increase with time, but with no distinct time trend (Fig 4.13). However, the survey in January 1997 especially yielded very low spine density estimates.

The mean length of the most distal spines was 1.2 ± 0.02 cm (S.E.) with a range of 0.05 cm to 5.56 cm. On the other hand, the mean length of spines most proximal to the second 'gall' was 1.9 ± 0.02 cm (S.E.), with a range of 0.2 cm to 6.4 cm. Spines up to 11 cm long were measured on some trees, although they were not part of the sample used in the analysis. Mean spine lengths of *A. etbaica*, *A. nilotica*, and *A. gerardii* were 5.0 cm, 7.0 cm, and 6.5 cm respectively (20 samples for each tree randomly measured from branches 150 cm above the ground) indicating that *A. drepanolobium* spines were much shorter.

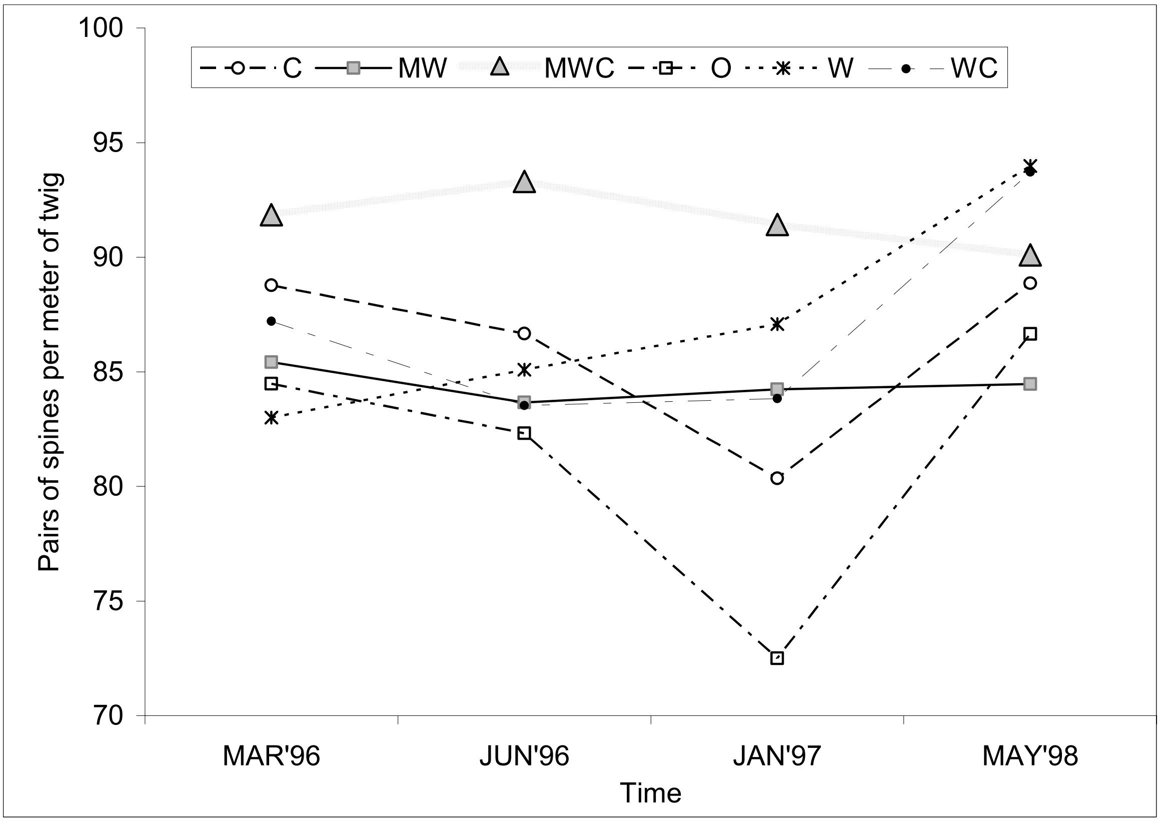

Fig. 4.13 Change in mean spine density (pairs of spines per meter of twig) of *A. drepanolobium* among herbivore treatments over time.

After showing a gentle increase between March ’96 and June’96, mean spine lengths of *A. drepanolobium* started decreasing with time among the different treatments (Fig 4.14; 415). The most distal spines showed a greater decrease compared with those most proximal to the second gall (Table 4.7).

Decrease in mean spine length was greatest in the cattle and total exclusion treatments and least in the mega-herbivore plots, although some trees in this treatment showed an increase in mean spine lengths. Spine length decreased by 20% in the cattle and total exclusion treatments, whilst increasing by 2% and 0.7% in the mega-herbivore and wildlife treatments respectively.

This observation is evidence of induced defences to herbivory. With the removal of herbivory, the need for mechanical defences of *A. drepanolobium* (spines) is probably relaxed. Additionally, it was found that the level of herbivory among *A. drepanolobium* trees was very low.

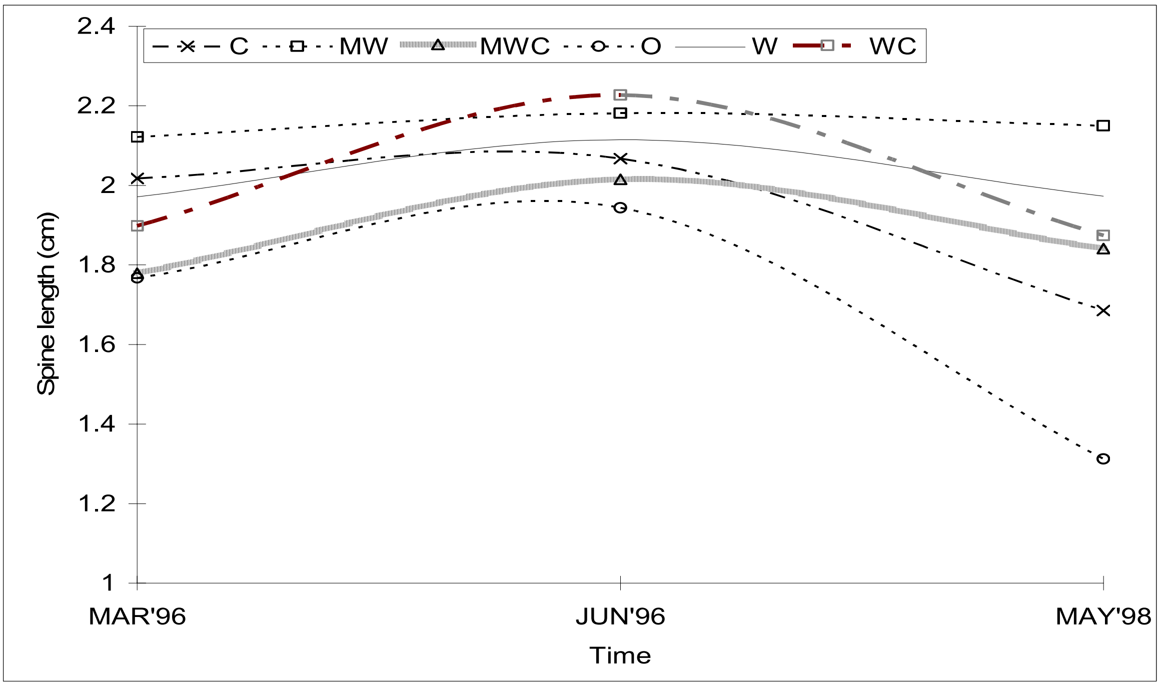

Fig. 4.14 Change in the length of spines most proximal to the second gall of *A. drepanolobium* trees among herbivore treatments over time.

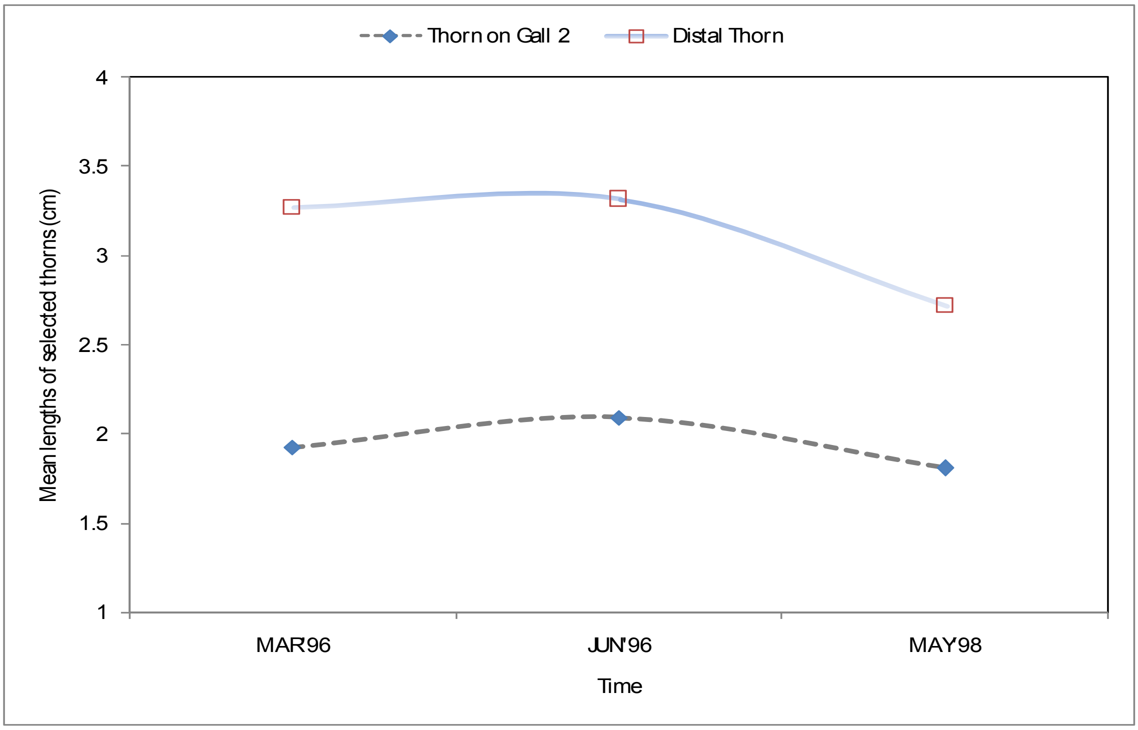

Fig. 4.15 Change in the mean length of spines most proximal to the second gall and at the most distal end of a twig over time.

Table 4.7 Changes in mean spine length (cm) (± S.E.) of the most distal spine and the spine most proximal to the second gall of *A. drepanolobium* trees, among herbivore treatments categorised by tree height classes between March 1996 and 1998

| | | 1996 | | 1998 | | Change (%) 1996-1998 | |
|---|---|---|---|---|---|---|---|
| Treatment | Height class | Distal spine | Spine proximal to $2^{nd}$ gall | Distal spine | Spine proximal to $2^{nd}$ gall | Distal spine | Spine proximal to $2^{nd}$ gall |
| MWC | < 50 cm | 1.2 ± 0.08 | 1.7 ± 0.10 | 0.8 ± 0.06 | 1.8 ± 0.13 | -26.90 | 5.95 |
| | 50 – 150 cm | 1.5 ± 0.16 | 1.6 ± 0.16 | 1.2 ± 0.15 | 1.9 ± 0.19 | -19.86 | 25.16 |
| | > 150 cm | 1.1 ± 0.10 | 2.1 ± 0.21 | 0.9 ± 0.09 | 1.8 ± 0.14 | -18.75 | -17.07 |
| MW | < 50 cm | 1.4 ± 0.10 | 1.9 ± 0.15 | 1.0 ± 0.07 | 1.8 ± 0.11 | -25.18 | -6.31 |
| | 50 – 150 cm | 1.6 ± 0.16 | 2.4 ± 0.20 | 1.0 ± 0.10 | 2.5 ± 0.24 | -35.67 | 4.25 |
| | > 150 cm | 1.4 ± 0.18 | 2.1 ± 0.18 | 0.9 ± 0.09 | 2.1 ± 0.24 | -38.46 | 3.41 |
| WC | < 50 cm | 1.3 ± 0.10 | 1.8 ± 0.16 | 1.3 ± 0.18 | 1.9 ± 0.22 | 0.76 | 5.68 |
| | 50 – 150 cm | 1.2 ± 0.10 | 1.8 ± 0.19 | 1.0 ± 0.11 | 2.2 ± 0.17 | -21.77 | 19.44 |
| | > 150 cm | 1.4 ± 0.14 | 2.1 ±0.30 | 0.9 ± 0.12 | 1.6 ± 0.19 | -37.96 | -25.24 |
| W | < 50 cm | 1.3 ± 0.12 | 1.6 ± 0.13 | 0.9 ± 0.09 | 1.7 ± 0.15 | -25.40 | 9.68 |
| | 50 – 150 cm | 1.6 ± 0.14 | 2.3 ± 0.19 | 1.3 ± 0.11 | 2.3 ± 0.18 | -18.62 | 3.11 |
| | > 150 cm | 1.3 ± 0.13 | 1.9 ± 0.13 | 0.9 ± 0.10 | 1.8 ± 0.19 | -31.8 | -6.18 |
| C | < 50 cm | 1.4 ± 0.13 | 1.9 ± 0.14 | 0.8 ± 0.08 | 1.4 ± 0.11 | -41.60 | -25.52 |
| | 50 – 150 cm | 1.5 ± 0.16 | 2.3 ± 0.16 | 0.9 ± 0.06 | 2.1 ± 0.21 | -43.05 | -8.00 |
| | > 150 cm | 1.4 ± 0.13 | 1.9 ± 0.17 | 0.7 ± 0.09 | 1.6 ± 0.13 | -47.44 | -18.42 |
| O | < 50 cm | 1.3 ± 0.11 | 1.6 ± 0.12 | 0.7 ± 0.08 | 1.6 ± 0.15 | -44.53 | 0.00 |
| | 50 – 150 cm | 1.3 ± 0.12 | 2.1 ± 0.17 | 0.6 ± 0.05 | 1.3 ± 0.22 | -51.14 | -36.71 |
| | > 150 cm | 1.1 ± 0.09 | 1.6 ± 0.15 | 0.7 ± 0.08 | 1.1 ± 0.12 | -37.03 | -33.54 |

Mean decrease in spine length was 14% for trees shorter than 50 cm tall, and 22% for taller trees in the cattle and total exclusion treatments. In treatments with mega-herbivores, trees less than 150 cm had a mean increase of 6%, but trees taller than this showed a 4% decline. Spines in wildlife (W), and wildlife and cattle (WC) treatments increased by 6% in length for trees less than 150 cm, but exhibited a decrease of 10% for taller trees. These results suggest little response in the spines of trees greater than 150 cm to the presence of herbivores.

A significant observation was that spines at the tips of twigs (distal spines) were not only shorter than spines at least 3-5 cm from the tip, but also showed the greatest decline in length. For *A. drepanolobium,* whose growing tips are most defended by the ants, is there a possibility that this greater ant presence has resulted in a reduced spine length? Grant's gazelle and giraffe that were seen browsing *A. drepanolobium* did so sporadically for a few minutes, though some Grant's gazelle and giraffe browsed entire new shoots. It is intriguing that spines at the most distal part of the shoot should be shorter than those in the-mid section, and even decrease in length by a greater proportion.

viii) Mortality of *A. drepanolobium* trees ranged from 1.7 to 8.3% between March 1996 and September 1998, or 0.9 to 4.2% annually (Table 4.8). The three blocks experienced similar mortality (F=0.28, P=0.76), indicating that whatever caused mortality was uniformly spread over the large experimental site. Treatments showed differences in percent mortality (F=9.16, P<0.000), with the wildlife treatment experiencing the least percent mortality. Mega-herbivores significantly contributed to mortality (F=27.66, P<0.000), in comparison to wildlife and cattle (Table 4.8).

Table 4.8 Mean percent mortality (± S.E.) of *A. drepanolobium* trees by height-class among herbivore treatments between March 1996 and September 1999. Means based on three replicates of 600 trees each. (Refer to Table 4.4 for treatment caption). Percent-annualised mortality is in the last column

| Treatment \ height class | < 50 cm | 50-150 cm | 151-300 cm | > 300 cm | Annualised mortality |
|---|---|---|---|---|---|
| MWC | 16.0 ± 4.26$^{ab}$ | 6.7 ± 2.89 | 2.7 ± 1.87 | 5.3 ± 2.61 | 4.0 |
| MW | 25.3 ± 5.06$^{a}$ | 4.0 ± 2.28 | 2.7 ± 1.87 | 1.3 ± 1.33 | 4.3 |
| WC | 14.7 ± 4.11$^{b}$ | 2.7 ± 1.87 | 4.0 ± 2.28 | 4.0 ± 2.28 | 3.3 |
| W | 6.7 ± 2.89$^{b}$ | 0.0 ± 0.00 | 0.0 ± 0.00 | 0.0 ± 0.00 | 0.9 |
| C | 12.0 ± 3.78$^{b}$ | 1.3 ± 1.33 | 1.3 ± 1.33 | 2.7 ± 1.87 | 2.3 |
| O | 12.0 ± 3.78$^{b}$ | 1.3 ± 1.33 | 1.3 ± 1.33 | 5.3 ± 2.61 | 2.6 |

Numerals with different superscripts within a column indicate treatments that are different (P=0.05). Differences were observed in the < 50 cm class only.

As expected, the mega-herbivore, wildlife and cattle treatment had significantly greater mortality compared with the total exclusion treatment (F=5.48, P=0.04), even though overall herbivory was low in all the study plots. Annual mortality in treatments with mega-herbivores was about 4%. On the other hand, mortality in the cattle treatments was similar to that of the total exclusion, suggesting that under conditions of little or no herbivory, annual mortality is less than 3.0%.

Mortality was greatest in trees less than 50 cm tall in all the treatments, accounting for between 52.2% (MWC) to 100% (W) of the mortality of all trees. Logistic regression did not demonstrate whether survival was a function of tree height. There was no evidence to suggest that the herbivores directly killed or destroyed any of the trees. A common denominator of all the big dead trees was the presence of a wood-boring beetle *Chrysobothris dorsata F.* (John Njoroge pers.comm.)*[1]*. The contribution of this beetle to the deaths was not ascertained. In cases where the woodborer was present and the trees were still alive, unidentified adult wasps from the family Braconidae, order Hymenoptera (John Njoroge pers.comm.) were seen eating the larva of the wood-boring beetle (*C. dorsata*). Lepidopteran larva from the family Noctuidae (P K Nderi pers. comm.)[2] were also found in the trunks of dead *A. drepanolobium* trees. (Both the beetle and the wasp are awaiting identification at the National Museums of Kenya). The parasitoid wasp was seen feeding on the larvae of the wood-boring beetle in trunks of five standing trees, and about 10 trunks of trees that had been felled. Conversely, it is possible that the beetles attacked

---

[1] John Njoroge, National Museums of Kenya, P O Box 40658, Nairobi, Kenya

[2] P K Nderi, National Museums of Kenya, P O Box Box 40658, Nairobi, Kenya

trees already weakened by other agents not yet identified. Furthermore, mega-herbivores and wildlife could have hastened the death of trees already weakened by the wood boring beetles.

### 4.4.6 Flowering, seedling recruitment and seedling survival

Very few seedlings were found in the experimental plots, therefore, the extrapolation to per hectare basis must be treated cautiously since this could mislead one to believe that such high recruitment rates were possible in an environment in which flowering hardly occurred. Mean percent survival ranged from 42% to 75% (Fig. 4.15). The cattle treatment recorded the greatest survival and wildlife and cattle treatment the least. Recruitment (new, emerging seedlings) was greatest in the mega-herbivore, wildlife and cattle treatment while no recruitment was recorded in the cattle treatment.

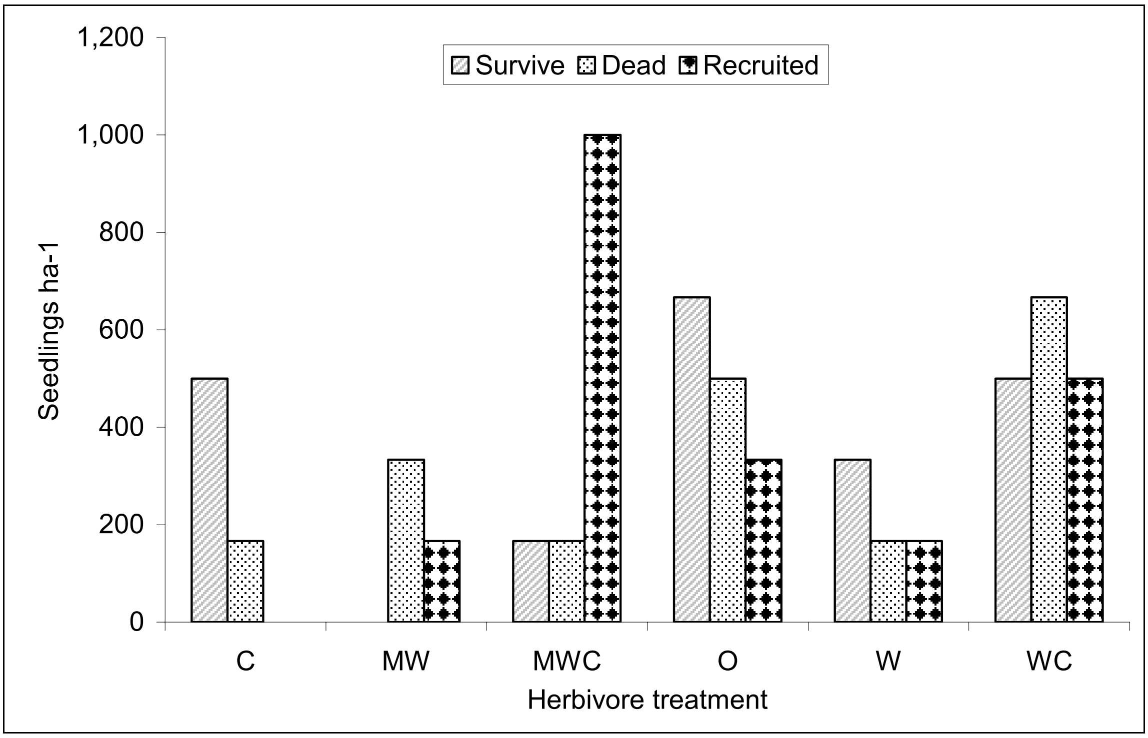

Fig. 4.16 Mean number of *A. drepanolobium* seedlings that survived, died and those recruited from September 1997 to September 1998 among herbivore treatments.

*Acacia drepanolobium* seedlings in this ecosystem did not survive for long. At least 25% died within a year of germination. However, those surviving are likely to more than replace any mortality on the bigger (more mature) trees whose mortality was about 3.0%.

Flowering was very sparse in the entire experimental area, and no reasons for this observation could be immediately mooted. No results of flowering, pod production and seed production are therefore, presented for the experimental plots. However, flowering of some *A. drepanolobium* trees took place on sites at least 2 km from the site. Flowering results are presented and discussed in chapter 5.

## 4.5 DISCUSSION: HERBIVORES AND WOODY DYNAMICS OF *ACACIA DREPANOLOBIUM*

### 4.5.1 Overstorey species composition, structure and dynamics

*Acacia drepanolobium* is the dominant tree species in this black cotton ecosystem. On the Mpala Research Centre, it comprised between 95% and 99% of the overstorey species' in areas with black cotton soil. Beentje (1984) and Coe & Beentje (1991) had reported that it is common on black cotton soils.

It may be tempting to infer that *A. drepanolobium* excludes other woody species to create an almost mono-specific stand because of the near absence of other woody species in this ecosystem. However, there was no evidence to suggest that *A. drepanolobium* in any way actively suppressed other woody species. In an on-going study (Young T. P & Okello B. D. unpublished data), it has been found that some of the other woody species are found in close proximity to *A. drepanolobium* trees only. However, the significance of this close association is still under investigation. Instead, it is suggested that the harsh environment of shrink-swell black cotton soils restricts the proliferation of other woody species.

The height structure showed a presence of all categories of heights, indicating that the heights were not uniform, an impression given by casual observation of the stands. The observed stand structures may be a product of the intrinsic growth rates of *A. drepanolobium* coupled with episodic recruitment. Episodic recruitment has been reported for *A. xanthophloea* (Young & Lindsay 1988). The observed clustering in certain height classes gives credence to the possibility of an episodic recruitment, or some disruption in growth, or recruitment, in the past.

The high overstorey density (about 2,000 individuals per ha) is an indicator of bush encroachment (Heady 1960), indicating favourable bush establishment conditions, inadequate numbers of browsers and/or infrequent fire for containing encroachment. High overstorey densities are also a manifestation of lack of active brush management like harvesting or fires. Dublin (1995) suggested that areas with high tree and shrub densities as in this ecosystem should be burned with hot fires because they were a big problem. High overstorey densities may lead to a change of understorey species. This was observed on a neighbouring ranch (Mogwooni) where only forbs and herbs were found under the interlocking canopies of *A. drepanolobium*, all the perennial grasses had disappeared. Such changes in understorey species composition are not good for the ranchers, since their livestock's forage is dependent on the presence of robust perennial grasses.

*Acacia mellifera, Cadaba farinosa, Rhus natalensis* and *Lycium europaeum* were the other important browse species with *C. farinosa* being the most common. An on-going study (Young T. P & Okello B. D. unpublished data) has established that in the absence of herbivory, these other woody species proliferate and are increasing in density. In this ecosystem, *L. europaeum* was found around termite mounds only, suggesting that it may require a specialised habitat in black cotton ecosystems. Okello (1996) reported that in the red soils of Laikipia, *L. europaeum* was common, and did not have any association with termite mounds. Fire is probably far more important than herbivory for the other woody species (Chapter 6).

### 4.5.2 Herbivory of *Acacia drepanolobium*

#### ***4.5.2.1 Herbivore density***

Herbivore dung density has been used to indicate the presence and also estimate the number of animals in a habitat (Therne 1982) and has been used to indicate the relative abundance of wild animals in Laikipia Kenya, (Okello 1996). The dung density results in this study confirm that at least 12 herbivorous mammals utilized the experimental plots by October 1996. Zebras were the most abundant and this is corroborated by total aerial counts of wildlife and livestock in the Laikipia ecosystem (DRSRS & MRC 1998). In this count, zebras were the most abundant in the entire Laikipia ecosystem.

Estimates of herbivore densities in the experimental plots were not made from the dung densities, but they can still be used as an index of herbivore presence (Therne 1982). The inference from the dung data is that only a few herbivore species used this range, in comparison to the total number of herbivore species in the ecosystem. Because of the low herbivore numbers, it is likely that the actual utilization of forage was relatively low, at least at the inception of the experiment. Secondly, it can be inferred that the experimental set-up worked well to exclude desired herbivore species. Thirdly, dung density has implications for nutrient cycling in this ecosystem. It has been postulated that treatments with greater dung densities could become more fertile (Young *et al*. 1995).

Only Grant's gazelles were seen frequently on the KLEE site, suggesting that there could be a resident herd. Elephant and giraffe, which can have profound effects on savanna vegetation (Pellew 1983; Ruess & Halter 1990; Dublin 1991), were few in number, probably because they have larger home ranges (Thouless & Sakwa 1995).

#### *4.5.2.2 Utilization of Acacia drepanolobium*

Though some ranchers had claimed that *A. drepanolobium* is of limited forage value, it is browsed by at least seven major herbivores (Elephant, giraffe, eland, Grant's gazelle, hartebeest, camel and goat) in Laikipia. Elephant, giraffe, eland, Grant's gazelle, and hartebeest were seen browsing in the experimental plots and, are therefore, responsible for the observed treatment differences in utilization. Grant's gazelle had the greatest dung density, and may be responsible for most of the observed utilization of *A. drepanolobium* trees.

Differences in utilization among the replicates can be ascribed to animal movements, which were beyond experimental control, but the difference in utilization among the treatments is attributable to access of the treatments as described in chapter 3, see also Appendix 1. The overall utilization recorded in the experimental plots was low, and utilization of *Acacia drepanolobium* was lower than that of other browse species present. These differences can be ascribed to the defences of the former species, comprising of spines (Milewski *et al*. 1987; Young 1987) and ants (Madden & Young 1992; Young *et al*. 1997; Stapley 1998). The other browse species may have spines and thorns, but not ants. Stapley (1998) demonstrated that *A. drepanolobium* twigs, from which ants had been removed, were more utilized than those with ants.

Secondly, herbivore density in the experimental plots was relatively low as indicated by the dung density estimates. Higher herbivore densities, especially of giraffe, have been reported to have significant effects on the density and structure of *A. drepanolobium* in El Karama ranch (Moore 1974). Moore (1974) reported that giraffe browsing significantly reduced the density and average heights of *A. drepanolobium*. In the nearby Ol Jogi private game sanctuary, giraffe had to be translocated to the livestock ranch when it became apparent that giraffe were decimating *A. drepanolobium* population (pers. observation). In both cases, trees were being reduced at a high rate (pers. observation). The populations of *A. drepanolobium* started recovering after the density of giraffe was reduced. However, evidence of the impact of giraffe is still evident to date even at El Karama ranch (pers observation).

These two examples show that with, or without, defences, *A. drepanolobium* is an important forage, especially for giraffes, and that at high enough densities, these browsers can effectively check its population. Pellew (1983) showed, in a model, that high densities of browsers such as giraffes, could wipe out the overstorey density in 10 years.

### 4.5.3 Growth characteristics of *Acacia drepanolobium*

#### *4.5.3.1 Vertical growth and increase in tree stem diameter*

The rate of growth recorded for *A. drepanolobium* (25 cm per year) is relatively fast for a hardwood species growing in a harsh environment, such as that found in the black cotton ecosystem of semi-arid areas. This environment is characterised by low annual rainfall, and soils that get water logged during rains and dry out and crack open during dry spells. The conversion efficiency was 0.33 mm per mm of rainfall.

The growth rates recorded compare favourably with the 33 cm per annum reported for *A. tortilis* (Pellew 1983) and the 19.1 cm per year (Birkett 2002) in a nearby sanctuary (Sweet Waters Tented Camp) in Laikipia. However, the stand studied by Pellew (1983) was mature (500 cm to 600 cm), where as the entire population (small to big trees) was sampled in this study. Some of the vertical growth is lost when the branches spread out and bend backwards.

Growth in stem diameter was relatively lower for *A. drepanolobium* compared to 8 mm for *A. seyal* (Hayashi 1992) and 5.24 mm for *A. tortilis* (Prins & Van der Jeugd 1993). However, *A. drepanolobium* is a relatively small tree in comparison with these two.

There is no plausible explanation for the differences in growth between treatments given the observed variation in both growth and RGR. However, it is significant that the wildlife-only treatment had the lowest RGR and cattle treatment the highest. The presence of wildlife seems to constrain the vertical growth of *A. drepanolobium*, while the presence of cattle and mega-herbivores seems to enhance it. It cannot be claimed that cattle enhanced the growth rates of *A. drepanolobium* in this ecosystem, and probably a longer period of monitoring is needed before a final conclusion is drawn.

Comparing the two extreme treatments (total exclusion (O) vs. mega-herbivore, wildlife and cattle (MWC)), suggests that herbivory does not negatively influence growth of *A. drepanolobium* at the current herbivore pressure. Therefore, keeping low densities of wildlife will not impact negatively on the population dynamics of *A. drepanolobium*.

The lower RGR in treatments that had wildlife, which included browsers like Grant's gazelle, eland, hartebeest and steenbok, suggests that these browsers may have directly or indirectly influenced growth of *A. drepanolobium* despite the relatively low utilization rates recorded.

Growth analysis by height classes indicated that the smaller trees, which are usually expected to show exponential growth rates (Harper 1977; Silvertown and Doust 1993), might have been suppressed. The vertical growth in the intermediate height classes was high, and conforms to the generally acknowledged theory that growth is exponential among smaller plants (Harper 1977; Hayashi 1992; Smit *et al*. 1996). Barring the large variations in vertical growth, the exponential growth phase in *A. drepanolobium* was between the 50 cm and 150 cm growth stages. Smaller trees could have been suppressed by competition from the herb layer, which at times exceeded 100 cm in height. Silvertown & Doust (1993) and Smit *et al.* (1996) suggested that grasses could suppress the growth of woody seedlings.

#### *4.5.3.2 Elongation of twigs*

As in vertical growth of the trees, herbivory did not show consistent or predictable effects on the growth of twigs. The strong seasonal influence in twig growth was expected because it is believed that rainfall events influenced their growth. Rainfall is one of the most important abiotic factors driving the growth of vegetation in savannas (Skarpe 1992; Prins & Van der Jeugd 1993; Smit *et al*. 1996).

Greater growth in twigs of *A. drepanolobium* in the cattle treatment compared with the wildlife treatment suggests that presence of cattle enhance growth in *A. drepanolobium.* Conversely, it is possible that wildlife negatively affects growth of *A. drepanolobium* trees. Reasons for the differences in twig growth among the herbivore treatments are not apparent. Compensatory growth after herbivory has been reported for *A. karroo* (Teague & Walker 1988; Du Toit *et al*. 1990) and *A. tortilis* (Pellew 1983), but herbivory was very low in this study. Moreover, cattle do not eat *A. drepanolobium* yet it had significantly higher twig growth than the wildlife treatment.

Mean growth in twig lengths translates to 27 cm per year in three years of above average rain. If these twigs do not die back, then a stage is set for bush encroachment by the tree canopies becoming larger (O'Connor 1996, 2000).

#### *4.5.3.3 Production of new shoots and shoot density*

At the same time, herbivory did not influence the production of new shoots in *A. drepanolobium.* The marginally lower density of new shoots in the cattle and total exclusion treatments indicates that herbivory played some role, but it is not easy to say which, and whether it was direct or indirect effects. However, the difference among the treatments with respect to total twig or shoot density suggests that herbivory may be important in influencing the longevity of the shoots. Such inferences have been made for *A. karroo* (Du Toit *et al*. 1990). It has been suggested that photosynthetic material of plants may live longer when browsed (McNaughton 1979). Again, the presence of ants probably made the suite of factors more complex. The fluctuation of shoot density over time can be ascribed to herbivory, rainfall and probably the ant species. Differential senescence of the twigs may also have played a role in the observed patterns.

### 4.5.4 Response of *Acacia drepanolobium* to herbivory

#### *4.5.4.1 Recruitment*

Many factors influence the recruitment dynamics of any woody species but flowering and seed production are the most important (Mucunguzi 1995). In the experimental plots, there was very little flowering and seed production (chapter 5). Seedling recruitment was thus very low. However, annual mortality of seedlings was equally low (25%), indicating a possible increase in bush densities if recruitment rates increase. High seedling survival rates coupled with low herbivory of seedlings and smaller trees also lend credence to this hypothesis. The study did not determine to what extent herbivores could influence seedling recruitment or survival, and hence, no strong inferences can be made.

Weltzin *et al* (1998) showed that herbivory by rodents and insects may constrain woody plant seedling establishment and stand development. These factors were not investigated in this study. However, the study area is rich in rodents, which have been found to feed on seeds of *A. drepanolobium* (Keesing 2000).

#### *4.5.4.2 Growth dynamics*

Evidence has been presented to indicate that herbivores (especially wildlife – W -) may influence growth dynamics of *Acacia drepanolobium*. The most noticeable response of *A. drepanolobium* to herbivory was increase in the number of twigs produced and hence increases in canopy volume.

#### *4.5.4.3 Bushiness[3] and encroachment*

Bushiness and encroachment can be analysed from a density or canopy volume point of view. In this study, density did not show any significant increase, but the tree canopies did. Increase in canopy cover attest to the increase in bushiness, especially when the concomitant increase in height is not matched. Higher seedling survival (despite the low recruitment levels) is also a strong indicator of increase in bushiness in this ecosystem. If canopy cover were to increase until the canopies interlock, a possibility given the density of trees here, the herb layer would be shaded out, and a change in herb-layer species composition would be inevitable (Smit *et al*. 1996). Already, some parts of Mogwooni ranch (less than 20km away) has this problem. The herb-layer species are basically forbs with no grasses.

Contradictory relationships between trees and the herb layer have been reported, e.g. *Panicum maximum* thrives under *A. tortilis* bush (Maranga *et al*. 1983; Kinyamario *et al*. 1995). Okello (1996) and Kinyua (1996) found *Pennisetum mezianum, P. stramineum,* and *T. triandra* thriving under canopies of *A. etbaica* and *A. tortilis* in the red soils of Mukogodo rangelands, but were almost non-existent in the open area away from the tree canopies. Trees in several savanna areas have been reported to contribute to a decline in herb layer production (O'Connor 1985; Belsky 1994; Scholes & Archer 1997).

Herbivores did not effectively suppress bushiness in this ecosystem, probably because of their low numbers. For herbivory to effectively impact on trees and shrubs, their numbers must be adequate (Pellew 1983). This has also been demonstrated by crashes in herbivore numbers following rinderpest outbreak in the Serengeti where tree and shrub recruitment closely follow herbivore population crashes and increases (Belsky 1984). In the Tsavo National Park, elephant poaching led to an increase in bushiness (Leuthold 1996), which was attributed to low elephant numbers. Lenzi-Grillini *et al*. (1996) concluded that the exclusion of grazing in the Queen Elizabeth National Park in Uganda resulted in high density of grass cover and bush thickets. Encroaching species are not good for the range because they can interfere with biodiversity (Steenkamp 1996).

Overgrazing by cattle has been alleged to be a major cause of bush encroachment (Pratt 1969; Prins & Van der Jeugd 1993; Smit *et al.* 1996), where grass over utilized, creating

---

[3] Bushiness refers to increase in the canopy volume and densities of the overstorey species.

room for the proliferation of trees and shrubs. Findings by Brown & Archer (1999) however, point to species specificity with respect to factors that drive encroachment in rangelands. Overgrazing results in fire suppression since the fuel loads are reduced (Heady 1960), and this may also contribute to bush encroachment. This study area was not subjected to overgrazing, and so the impact of cattle was low. But, the greater increase in canopy of the total exclusion treatment indicates that bushiness can increase even without cattle or other herbivores (Okello 1996). Thus, a delicate balance in the levels of herbivory should be found and maintained to ensure that bush encroachment is controlled.

Trees surveyed for canopy cover were initially 300 cm or shorter, and though some grew much taller with time, the present results do not describe the canopy dynamics of much taller trees, although they would be expected to follow the dynamics reported, normal of an increase in cover, and hence bushiness.

### 4.5.5 Defence against herbivory

Defence against herbivory in *A. drepanolobium* was a significant finding in this study. *Acacia drepanolobium* has at least two defence mechanisms available against herbivory. Firstly, spines and thorns defend *A. drepanolobium*, spines being ubiquitous in African *Acacia* species (Ross 1979). Secondly, belligerent ants that occupy the swollen thorns of this tree species also play a defensive role (Madden & Young 1992; Young *et al*. 1997).

#### *4.5.5.1 Induced defence and density of spines*

Changes in spine length and spine density corresponded with the expected herbivory presence in different treatments. Though spine density (number of spines per unit of twig length) was greatest in the mega-herbivore, wildlife and cattle treatment, there was a general decrease in spine density with time.  Spine lengths also showed a similar decline over time. These two results suggest that *A. drepanolobium* relaxed its induced defence (thorn length and thorn density) as herbivore pressure was reduced, although in a gradual manner. It is expected that this relaxation may continue to at least a 50% reduction in spine length in trees within plots protected from browsing. Many *Acacia* trees and shrubs (e.g. *A. etbaica*, and *A. nilotica*) that have evidently been protected from herbivory have never lost all their spines, and a similar response is expected in *A. drepanolobium* – a partial but not total – reduction in the spine lengths and density. However, Fig. 4.5 demonstrates that some herbivory may take place even in protected treatments, resulting in a non-consistent response on spine lengths. (See also Appendix 2). This observation is evidence of induced defences to herbivory. With the removal of herbivory, the mechanical defences of *A. drepanolobium* (spines) are relaxed.

#### ***4.5.5.2 Defence by ants: density of galls***

Ants that occupy the swollen thorns swarm any strange body that comes into contact with the tree. During daytime, most are found around new growing tips where they bite and sting intruders. These ants therefore act as deterrents to herbivores, and can be regarded as part of *A. drepanolobium* anti-herbivore defence mechanism (Madden & Young 1992; Young *et al*. 1997; Stapley 1999).

If this is the case, with other factors constant, the more ants the better the defence, implying that if housing (galls) for the ants were not limited, the defence would be enhanced. However, the swollen thorns in *A. drepanolobium* are not true galls because ants or other herbivores do not induce their production. *Acacia drepanolobium* seedlings in a green house (see chapter 5) produced galls even in the absence of ants.

The two defence mechanisms complement each other. The spines make access to browse difficult, while the belligerent ants ward off any persistent browsers. Defence by the spines is induced (Midgley & Ward 1996) and meets the three criteria proposed by Karban & Myers (1989) for induced defences. These are, i) the response is associated with herbivory, ii) the response actually reduces herbivory, and iii) reduced herbivory increases the fitness of the plants. For *A. drepanolobium*, Milewski *et al*. (1991) provided evidence for all these criteria, and the results from this study confirm this.

This study has directly met the first two criteria, while the high growth rates of twigs in the cattle and total exclusion treatments suggest a greater fitness. Pellew (1983) had experimentally demonstrated that herbivory by giraffes dramatically reduced growth of *A. tortilis* an effect also reported by Moore (1974) for *A. drepanolobium*. It is acknowledged that herbivory pressure was too low for dramatic results, especially on fitness of the tree to be detected within the data collection period. It is clear that *A. drepanolobium* in the total exclusion and cattle treatments (C) had shorter spine lengths compared with those in the mega-herbivore, cattle, and wildlife treatments (MWC).

If herbivory induces spinescence, then its absence should relax it, and this meets the first criteria. Milewski *et al*. (1991) and Stapley (1999) have shown that the spines in *A. drepanolobium* significantly reduced herbivory by goats. It is important to note that the changes in spinescence (spine density and spine length) are permanent over that period of time or season. Spines are produced during each season, and there may be a time lag before plants respond to the levels of herbivory. It is also possible that the plants may be 'cautious' to react to sudden changes in the levels of herbivory, and may respond only after long periods during which, the prevailing levels of induced defence are maintained. These results provide empirical evidence that mean spine length in *A. drepanolobium* is positively associated with variation in browsing by native herbivores. The great variation in spine lengths among trees within plots could be a result of past herbivory.

Some of the variability observed among trees, which, confounds the observed treatment effects is related to the species of resident ant. For instance, spine density and spine lengths were significantly different among the ant species (chapter 8).

Janzen (1966) and Madden & Young (1992) adduced evidence that *Acacia* species defended by resident ants, may have fewer alternate defences than acacia species without ants. The shorter mean spine lengths of *A. drepanolobium* compared to the heavily browsed *A. nilotica* and *A. gerardii* are examples. Though spine densities of the latter trees were not estimated, their lengths were much longer, suggesting their importance in discouraging browsing.

The current results suggest that either mammalian herbivores, or the ants, play a role in the density of swollen thorns produced. Data from this study was not conclusive on the role herbivory plays a role in the increase in gall density and therefore ant activity. Similarly, it is not clear whether the presence of ants would lead to more galls, and enhanced defence. (See more details on ants in chapter 8).

### 4.5.6 Mortality

*Acacia drepanolobium* may maintain a seedling bank as opposed to a soil seed bank. Many young trees were found in the 'seedling' stage (a state where young or small trees stay in an almost stagnated form and were then released to grow after few months or even years) and a few were released to establish. Establishment was apparently suppressed by the enormous biomass of the herb layer. In the exclosures, there was very little seedling recruitment, which was attributed to lack of flowering for a long time. At least 25% of the seedlings recruited died within the year. Mortality was greater in the mega-herbivore, wildlife and cattle treatment compared with the rest of the treatments although this could not be tested statistically because of the very low number of seedlings recruited. Possibly, animals in this treatment contributed to the mortality by trampling the seedlings to death.

Rodents have also been known to stifle seedling recruitment and establishment in *Prosopis sp.*(Giannoni *et. al.* 2005)

Mortality amongst the established trees was low, about 3% per annum compared with 8-10% reported for *A. tortilis* (Weyerhaeuser 1982) in Lake Manyara Reserve, which, however, was recorded for a population that was heavily impacted by a high elephant density. Birkett (2002) estimated mortality of protected *A. drepanolobium* to average 0.4% annually, but an average of 12% in the presence of mega-herbivores. It is suspected that other than old age, mortality among the established trees was at least in part correlated to the presence of the beetle *C. dorsata* and larva of a Lepidopteran in the family Noctuidae. The beetle could have weakened the tree and left it susceptible to other agents of mortality. However, all the dead trees had hollow stems, with numerous beetles. It is also possible that the beetle attacked trees that had already been weakened by other agents of mortality. None of the dead trees had signs of injury caused by large mammals. The seedlings that survive are likely to more than replace any mortality amongst the bigger (more mature) trees where mortality was about 3.0%. It is also probable that some trees died as a result of self-thinning (Harper 1977), given the high tree densities. Dublin (1995) attributed seedling mortality in the Mara ecosystem to the following agents, i) 4 % to elephants, ii) 4 % to fire, iii) 1 % to wildebeest and iv) 1 % to natural causes.

### 4.5.7 Summary

This study has shown that *A. drepanolobium* has varied maximum heights, and a mean vertical growth rate of 24.9 cm $yr^{-1}$, which is greatest among medium sized trees. Increase in girth averages 0.73-0.81 cm $yr^{-1}$. The results were not conclusive on the effect herbivores have on growth, but it is suggested that herbivores (especially browsers like elephant and giraffe) can and do have profound effects on growth of *A. drepanolobium*, if they are present in sufficient numbers. Apart from herbivores, other factors that influence the growth of this tree include rainfall (because of the seasonal growth patterns) and probably acacia ants (chapter 8).

As the tree grows, so it increases in canopy volume and bushiness. Treatments that were not subjected to any browsing pressure had greater canopy volumes than those without. This also indicates that browsing herbivores play an important role in the bush-encroachment dynamics within the ecosystem.

Herbivory of *A. drepanolobium* within the experimental units was low compared with the other browse species, suggesting that *A. drepanolobium* is not among the most preferred browse species. This observation has been attributed at least in part to the presence of belligerent acacia ants.

Though herbivory levels on *A. drepanolobium* were low, the influence of browsing herbivores was prominent in the relaxation of spinescence. Treatments without browsing herbivores recorded a significant decrease in spine length, suggesting that this physical defence mechanism is induced.

Survival rate of *A. drepanolobium* were high. However, survival was also influenced by the presence or absence of browsers. Most of the mortality was recorded among small trees, which also suggests that factors other than herbivory played a role.

The most startling finding was the lack of flowering among *A. drepanolobium* trees over a three-year period, and significantly, this was restricted mainly around the experimental unit. The seed bank was poor (chapter 5), and this contributed to the low number of seedlings. It is, therefore, hypothesised that seedling recruitment may be episodic, and closely follows flowering events. It is further suggested that the *A. drepanolobium* soil seed bank does not exist for long periods, a situation that is not uncommon in the genus *Acacia*.

Data from this study did not conclusively and consistently demonstrate the effects of herbivory on the population dynamics of *A. drepanolobium*. However, different categories of herbivore (e.g. mega-herbivores versus small bodied browsers) have different effects on the population dynamics of *A. drepanolobium*.

As demonstrated in chapter six, fire has a more profound effect on the population dynamics of this tree than herbivores. Although the fire experiment suggested that *A. drepanolobium* may have adapted to fire, the defoliation effect of fire on the tree remained quite significant. Results from chapter five also confirm this thinking, because fire significantly contributed to reduced germination of *A. drepanolobium* seeds.

# 5 CHAPTER FIVE: SEED ECOLOGY OF *ACACIA DREPANOLOBIUM*

## 5.1 INTRODUCTION

*Acacia* species are plants of immense economic value in the arid and semi-arid rangelands of Africa because they provide *inter alia*, forage, fuelwood, habitat for animals and timber (Buech & Rugg 1985; Lamprey 1986). *Acacia* species also play an important role in savanna vegetation dynamics, especially when their densities increase and they become a bush 'problem' (O'Connor 1996). Bush encroachment in arid and semi-arid rangelands has now assumed global significance (Kriticos *et al.* 1999) and invariably results in reduced herbaceous production (Sabiiti & Wein 1988; Sabiiti *et al* 1991), though not exclusively so (Cavanagh 1980; Belsky 1990). Reduced herbaceous production results in lower animal (wild and domestic) production (Mbuvi & Croze 1986). Most bush encroachment has been blamed on overgrazing especially by cattle (Walker *et al*. 1981). However, even under-grazed rangelands often have bush encroachment problems (Okello 1996).

In the Laikipia plateau of central Kenya, *Acacia drepanolobium* is the most important woody species in upland areas with black cotton soils. Many ranchers in Laikipia have labelled *Acacia drepanolobium* as a problem species because it a) coppices readily in response to top kill by fire or harvesting; b) is of low forage value since it is heavily defended against herbivory by ants and spines; c) is increasing in density within its stands and probably expanding into open grasslands, and d) has not been successfully controlled by chemical and physical means. Many elderly people from Laikipia (especially amongst the Maasai and Turkana communities – pers. comm.) have corroborated this by pointing out many areas at Mpala that were hitherto open grasslands but now have high densities of *A. drepanolobium.*

Many *Acacia* trees and shrubs regenerate both vegetatively (Purdie & Slaytor 1976; Jacoby 1986; Hodgkinson & Oxley 1990) and from seed (Oba 1990), the latter being the dominant mode (Mucunguzi 1995). Germination and seedling establishment can be influenced by fire (Hodgkinson & Oxley 1990; Portlock *et al.* 1990), temperature (Hodgkinson 1986), soil moisture (Hodgkinson & Oxley 1990), seed coat thickness (Fenner 1986), predation (Sabiiti & Edroma 1991), competition (Cavanagh 1980), intrinsic ability of a species to germinate and establish (Fenner 1986), seed size (Mucunguzi 1995), and shape (Cavanagh 1980). Most seeds of indehiscent *Acacia* species need a pre-sowing treatment before germination (Lamprey 1967), but many dehiscent species germinate freely without pre-sowing treatment, especially if they are fresh (Cavanagh 1980). Some species germinate after a fire (Hodgkinson & Harrington 1985). These factors may reflect the means by which the two types of *Acacia* species (dehiscent and non-dehiscent) are dispersed. Most dehiscent species are dispersed by wind, while indehiscent ones are mostly dispersed by herbivores.

Rangeland scientists and managers need to understand the underlying processes involved in bush encroachment at various levels, from species to landscape level, in order to mitigate the effects of bush encroachment (Roques *et al* 2001). Increase in density of woody species cannot start without seedling recruitment, the most critical phase in seedling establishment, which depends on the availability of seeds (Smit *et al.* 1996). Emergence from seed is the primary means by which most *Acacia* trees and shrubs propagate themselves (Mucunguzi 1995). Therefore, investigating the seed ecology of suspected invader species is an important step towards better understanding of these processes in order to formulate suitable management options.

Understanding the population dynamics of a species cannot be complete without a clear knowledge of its seed ecology, which is also invaluable in planning the introduction of new species for commercialisation and other uses. Knowledge of the seed ecology of *A. drepanolobium* will therefore contribute towards understanding the factors that contribute to its tag of being a bush encroachment problem, as well as offer insights on how to mitigate such effects.

The three main sources of seeds that germinate in savannas include freshly produced seeds, dispersed seeds and soil seed banks. Seed banks are influenced by; seed production, dispersal, seed predation, seed longevity, germination, and seed mortality, among other factors (Harper 1977). Rapidly germinating or establishing seeds are likely to have few, if any, seeds in the seed bank but greater chances of establishing (Fenner 1986).

Seed availability depends on reproductive output, which in turn is usually positively dependent on tree size. Potentially available seeds are threatened by predators such as bruchid beetles (Miller & Coe 1993), mammalian herbivores (Miller 1994a), and agents of mortality such as fire (Cavanagh 1980).

Seeds of almost all *Acacia* species are consumed or attacked by bruchid beetles (Miller & Coe 1993; Miller 1995), and an *Acacia* species may be attacked by one or a number of Bruchid species (Coe & Coe 1987). The number of bruchid species that attack any *Acacia* species tends to be proportional to the seed size (Halevy 1974). The extent of destruction of the seed and food reserves by bruchid beetles and, by implication, seed size, are important in seed viability after bruchid attack (Lamprey *et al.* 1974). Seeds germinated after the first instar larvae are likely to have a higher germination rate than those in which adult bruchid beetles emerge.

Fire is a frequent occurrence in East African savannas (Wein & Edroma 1986) and it is one of the most potent environmental factors shaping the structure of its vegetation (Oba 1990). Fire events may stimulate (Hodgkinson & Harrington 1985) or enhance (Pratt & Knight 1971; Hodgkinson & Oxley 1990) germination of some tree and shrub species. Fire may also inhibit germination and stifle seedling establishment of some *Acacia* species by killing them (Cavanagh 1980). Fire has, therefore, been used as a tool in range management by pastoralists, ranchers, and scientists (Hodgkinson 1986; O'Connor 1985). The effect of fire on the germination and seedling establishment of any species will depend on physiological and morphological adaptations to fire (Oba 1990; Hodgkinson 1986; Hodgkinson & Oxley 1990), the amount and type of fuel used, the frequency and intensity of fires (Noble *et al,* 1986; Belsky 1990) and the type of fire (Trollope & Trollope 2002).

Pastoralists in East Africa frequently burned *Acacia*-dominated woodlands as a bush control measure and also to enhance fresh growth of graze forage (Pratt & Gwynne 1977; Pellew 1983). However, fires have become infrequent in the East African rangelands, including the study site.

*Acacia drepanolobium*, like *A. karroo* in South Africa, does not match the profile of other known invader *Acacia* species like *A. nilotica* and *A. tortilis*. The latter are indehiscent and heavily browsed by herbivores, whereas *A. drepanolobium* is not although *A. karroo* is heavily browsed. *Acacia drepanolobium* is a soft-seeded species with a thin seed coat.

This chapter reports on the flowering, seed production and germination of *A. drepanolobium*. The effect of acid scarification on germination of *A. drepanolobium* was assessed and the hypothesis that fire and bruchid infestation enhance germination of *A. drepanolobium* was tested. Seedling establishment and survival of *Acacia drepanolobium* in different soil types was investigated to test the hypothesis that *A. drepanolobium* is specialised for germinating and establishment in black cotton soils.

## 5.2 OBJECTIVES OF INVESTIGATION

With the goal of understanding the seed ecology of *A. drepanolobium*, the specific objectives of this chapter were the following:

1. Determine the degree of flowering and seed production of *A. drepanolobium*;

2. Investigate the influence of bruchid beetle infestations the germination rates of *A. drepanolobium* ; and

3. Determine the seedling establishment and survival of *A. drepanolobium* on different soil types.

## 5.3 MATERIALS AND METHODS

### 5.3.1 Flowering, pod and seed production of *Acacia drepanolobium*

The study area and species have been described in Chapter 3. The 1,800 *A. drepanolobium* trees tagged in the KLEE experiment (see Section 4.2.4) were used to monitor flowering and pod production. Because no flowering took place over a 14-month period within this experimental unit, two other sites located two and five kilometres away respectively (Fig. 3.1), were used to determine percentage of trees flowering and their seed production.

In the site about 2 km away from the KLEE experiment, only flowering and pod production were monitored in 180 trees. The seeds that were harvested from trees earmarked for destructive sampling in this site were discarded when it became apparent that some seeds could have been re-infested by bruchid beetles while in storage. But this data is quite revealing in terms of flowering and seed production on trees with different resident ant species (chapter 8).

In the third site five kilometres away, three randomly placed 5 by 30 m transects (mean density 689 trees ha$^{-1}$), which is slightly more than a third of 2,200 trees per ha recorded in the KLEE experiment, were tagged and measured for height, diameter and crown cover. The sample size was 31 trees. The resident ant species in each tree was also recorded. Trees were categorised into classes of (i) flowering, (ii) flowering and pods present, (iii) pods only, and (iv) no flowering, no pods. All the pods in each tree were harvested in the morning and the pods placed in labelled polythene bags.

### 5.3.2 Bruchid infestation and seed depredation

The pods of each tree were counted and weighed, seeds were then separated out, counted and weighed. Seeds were visually examined for signs of infestation and other forms of injury. Seeds judged as good were thoroughly screened for the presence of bruchid beetles and other signs of predation or damage by examining them under a binocular/dissecting microscope at X 40 later that afternoon. As this examination was time consuming, a sub-sample (about 25% of the sample size) was used for 26 out of the 29 samples. Samples of bruchid beetles were taken to the National Museums of Kenya for identification.

To determine whether goats could disperse *A. drepanolobium* seeds, a goat was fed on *A. drepanolobium* branches that had mature pods for over 60 hours in an enclosed room. All the faecal droppings were recovered over 7 days and washed through a sieve. However, no seeds were recovered. Ten piles of dung each from elephant, eland, hartebeest and Grant's gazelle were collected from *A. drepanolobium* wooded lands and passed though sieves and examined for presence of *A. drepanolobium* seeds.

### 5.3.3 Soil seed bank

Soil for estimating the size of *A. drepanolobium* seed bank was collected from three sites with *A. drepanolobium* trees in June 1996. In each of the three sites, nine samples were collected from the top 15-20 cm within an area of 10 m$^2$. The first site had black cotton soils, the second was intermediate between black and red luvic soils (hereafter loam soils) and the third had red luvic arenosols or red soils (Ahn & Geiger 1982). *Acacia drepanolobium* had flowered and produced pods only in the loam soil.

Half of each soil sample was placed in labelled germination trays and watered for four weeks to allow for germination of seeds. The other half was washed out in water and passed through sieves to extract any seeds. All the seeds collected were compared with known seeds of *A. drepanolobium* that had been collected earlier, but none were *A. drepanolobium*. Subsequent germination and establishment tests of the recovered seeds yielded only forbs. Seedlings that emerged from the germination trays were forbs, grasses, and seedlings of *A. brevispica* (especially from the red luvic arenosols). Because no *A. drepanolobium* seeds were recovered from these soils, the soils were deemed to be devoid of *A. drepanolobium* seeds.

### 5.3.4 Seed germination and establishment

Seeds of *A. drepanolobium* were harvested from trees with mature pods at Mpala between May and July 1996. The seeds were sorted into damaged and undamaged seeds by examining them for the presence or absence of bruchid entry and exit holes, and ant damage to the seed testa under a microscope. The seeds were stored in polythene bags and the undamaged ones examined again for signs of damage after two weeks.

### 5.3.5 Effect of pre-sowing treatment by 1M hydrochloric acid and fire on the germination of *Acacia drepanolobium*

A pilot experiment was carried out to determine whether seeds of *A. drepanolobium* need an acid pre-sowing treatment, and to gauge the germinability of its fresh seeds. The objective of this experiment was to prepare for the subsequent experiment below.

A light grass fire (150g of dry grass) was passed through a batch of 200 undamaged seeds placed on the ground to obtain burnt seeds. Of these seeds, 120 were randomly picked and divided into two lots of 60 seeds each. Another batch of 120 bruchid-damaged seeds were picked and similarly divided into two equal batches. A third lot of 120 normal beetle-free, unburned (control) seeds were also divided into two equal lots. One set of the three treatments was separately immersed into jars containing 1M HCL for five minutes and then rinsed with rainwater.

The two sets, acid treated and acid free, were then germinated on filter paper lined trays. Each filter paper had twenty seeds. Scarified and non-scarified seeds were germinated on separate trays. The trays were wetted with water on a daily basis and covered with a polythene bag to keep the trays moist. The germination trial was conducted inside a screen house where the temperatures ranged from a minimum of 17°C to a maximum of 33°C. Germination was recorded daily for thirteen days. Germination was deemed to have occurred when the radicle extended to 2 mm. After 13 days all the seeds that had not germinated were found to have rotted and were discarded.

### 5.3.6 Effects of fire, bruchid seed beetles, and soil type on germination and seedling establishment

Three soil types (see section 5.2.3) were collected to a depth of 20 cm and put in wooden germination crates. The crates were 50 cm X 50 cm X 15 cm deep, and were subdivided into 49 equal squares using nylon fabric. These crates were watered daily for two months in order to deplete the existing soil seed bank while examining for the presence of *A. drepanolobium* seedlings.

Emerging seedlings were mainly herbs and *A. brevispica* from the red sandy and clay loam soils, and were all were removed. A total of 27 crates were used in nine treatment combinations each replicated three times. The treatments were; 1) burnt seeds, 2) bruchid-damaged seeds, and 3) undamaged (control) seeds in each of the three soil types in a modified factorial design (burnt bruchid-damaged seeds were not included as a treatment). One seed was planted to a depth of 1 cm in each of the 49 squares in all the crates, giving 147 seeds in each treatment combination (1,323 seeds in total). For seven days, germination was recorded daily by observing for emergence of the plumule. After the first seven days, germination and seedling growth, measured by increase in heights to the nearest 0.1 cm were recorded on a weekly basis. The germination crates were watered twice a week for the entire duration of the experiment.

### 5.3.7 Effect of fire on the germination of surface placed, and buried *Acacia drepanolobium* seeds

*Acacia drepanolobium* seeds were germinated within the burn plot (see chapter 6 for experimental design) to determine the potential effect of fire on *A. drepanolobium* germination under field conditions. At each of ten randomly selected positions within the burn plot, four contiguous 1 $m^2$ plots were laid out. On two of these, 100 *A. drepanolobium* seeds were placed on the surface and their positions on the ground marked with coloured pins. In the other two quadrats, an equal number of *A. drepanolobium* seeds were planted just below the soil surface and their positions similarly marked with coloured pins. From each of these two treatments (surface and planted), one set of seeds was recovered and taken for screen house germination on filter paper lined trays a day after the burn. The other set was left to germinate in the field and its germination monitored weekly for three weeks. Seeds that had germinated were marked with typists' correction ink to avoid double counting.

### 5.3.8 Data analysis

a). Flowering, pod and seed production

The probability of a tree flowering in relation to height was analysed first by logistic regression followed by linear regression using JMP-IN (Sall & Lehmi 1999). The effect of resident ant species on the probability of a tree flowering was analysed by log-likelihood chi-square ratio. Flowering in the KLEE experiment was analysed by ANOVA 1, and linear contrasts done between treatments with mega-herbivores and those without, cattle versus wildlife and herbivores versus no herbivores.

The relation between the mean number of pods produced and tree height were analysed first by logistic regression followed by linear regression. Transformation of pod and seed numbers, and pod and seed weights to logarithms and square roots did not improve the regression.

b). Pilot germination experiment

This was a nested experiment (Steel & Torrie 1980), with the acid being the major treatment, while burnt and damaged seeds as the minor treatments. Analysis of variance was done using Systat® software (SSI 1996) to determine whether acid scarified seeds were different from non-scarified seed, and whether bruchid beetles and fire had any effect on the germination of *A. drepanolobium*. The data was log-transformed from the percentage germination figures.

c). Effects of fire, bruchid seed beetles, and soil type on germination and seedling establishment

The analysis of variance was done using a modified factorial design because burned damaged seeds were not included.

The effects of fire, bruchid infestation and soil type on germination were analysed separately and means differentiated by Tukey’s post hoc test using Systat® software (SSI 1996).

## 5.4 RESULTS

### 5.4.1 Flowering and pod production

Flowering of *A. drepanolobium* generally starts a few days before rains fall. Rainfall at Mpala is quite variable in space and time (Fig. 3.3), and growth continues through the rainy period. Some trees remain in flower even long after the rains, suggesting a staggered flowering regime. Pods are produced three or four weeks after flowering starts. In some sites that were not sampled, *A. drepanolobium* flowered three times in a year, with flowering tracking the rains, suggesting that *Acacia drepanolobium* may be an indicator of rainy seasons.

Flowering of *A. drepanolobium* trees within the KLEE site was low, being greatest in the cattle treatment (2.0 ± 0.65% S.E.), compared with the mega-herbivore, wildlife and cattle treatment (0.8 ± 0.65% S.E.) with no significant differences among the treatments (F=0.6, P=0.72). Linear contrasts did not show any significant treatment effect that could be ascribed to the presence or absence of any herbivore suggesting that the current levels of herbivory did not influence the flowering of *A. drepanolobium*. Logistic regression showed that tree size significantly ($P < 0.001$) influenced flowering. No tree less than 50 cm in height flowered, while 3.8% of trees in the > 300 cm class flowered.

In the site 2 km away from KLEE, the proportion of trees flowering was 48.2 ± 4.4% (S.E) in October 1997, 22.7 ± 5.0% in February 1998, and 47.9 ± 5% (S.E.) in August 1999, an average of 40.3 ± 3.3% and were different (F=8.94, P<0.001). The low flowering recorded in February 1998 was ascribed to the heavy rains (El Nino) that were still falling at the time of sampling leading to prolonged water logging. These results indicate that *A. drepanolobium* population can flower in different seasons during the year. However, none of the tagged trees flowered more than once a year.

Trees with *Crematogaster mimosae* ants were more likely to flower ($P < 0.05$) compared with trees that had *C. nigriceps* or *Tetraponera penzigi*. At least 68.9% of all *C. mimosae* colonized trees flowered compared to only 5.8% for *C. nigriceps* while *T. penzigi* and *C. sjoestedti,* which were least abundant, had 43.2% and 61.8% of the trees they occupied in flower respectively.

Logistic regression showed that height was a factor in flowering. Most trees that flowered produced pods or fruits soon thereafter. However, it was not confirmed whether all the pods had seeds. Tree heights ranged from 65 cm to 275 cm. The shortest tree that had flowers and pods was 70 cm. The pod and seed yields from these trees were not measured since another on-going experiment was using the same trees. The probability of *A. drepanolobium* trees flowering and producing pods depended on the resident ant present and the height of the tree it occupied (Chapter 8).

Flowering in the site 5 km away from KLEE was high with 29 (93.5%) trees in flower and, of these, 28 (96.65%) produced pods. Tree density was low, 689 trees per hectare compared with 2,200 for the KLEE. Mean pod production was 2,170,000 pods $ha^{-1}$ for the observed density or 0.13 kg per tree, which translates to 86.8 kg $ha^{-1}$. The mean number of seeds per pod was 3.1 ± 0.17 (S.E), n=28. Though the sample size was small (31 trees), the number of pods produced, the weight of pods and seeds had a strong and positive linear relationship with the tree density ($R^2$ =0.77, $R^2$ =0.81 and $R^2$ =0.81 respectively). Similarly the number of pods was positively related to the mean crown diameter ($R^2$ = 0.77) implying that trees with a larger crown volume are likely to produce more pods and hence seeds. However, the relationship between height and pod production was poor with only 29% of the variation accounted for. This can be ascribed to the small sample size, and the limited range in height variation (95 to 205 cm) of the sampled trees. At least 32% of the variation was accounted for when weight and not number of pods was used in the analysis. There was a linear fit between number of seeds and number of pods (square root transformed) $R^2$ = 0.93.

### 5.4.2 Seed infestation and depredation

The bruchid beetle that infests *Acacia drepanolobium* seeds was identified at the National Museums of Kenya to the genus level as *Bruchus* sp. (Michael Mungai[4], pers. comm.). Only one species was found, and each seed of *A. drepanolobium* was attacked by only one individual of *Bruchus* sp. The adult *Bruchus* sp. leaves a large deep hole (almost three-quarters of the seed surface on one side) upon emergence. The adult emerges after eating up most of the seed contents.

Between 30% and 100% of all seeds were infested, in the most part by bruchid beetles. The cause of damage in seeds that were visibly damaged or had holes could not be ascertained, and can be ascribed to both bruchid beetles and herbivory by the resident

---

[4] Michael Mungai, National Museums of Kenya, P O Box 40658, Nairobi, Kenya.

ants. All the damaged seeds that were examined under the microscope had bruchid beetles in various stages of development. Mean infestation was 67.2 ± 3.29% (S. E.)

In another experiment (see section 5.3.3 (c) on fire germination experiment below), 72% of buried seeds were recovered. Since most of the recovered seeds were intact and had not been burned, it can be safely assumed that the missing ones were predated upon, and the pouched mouse *Saccostomus mearnsi* (Keesing 1998, 2000) is the prime suspect.

No seeds were recovered from the dung pellets of a goat that was fed on *A. drepanolobium* leaves and pods for over 60 hours. However, intact seeds were recovered from undigested pods in three balls of elephant dung piles (out of ten piles) while crushed seeds were found in eland and Hartebeest dung, suggesting that these herbivores play some role in the dispersal of *A. drepanolobium* seeds. No seeds were recovered from the dung of Grant's gazelle, which are common in *A. drepanolobium* woodlands.

### 5.4.3 Soil seed bank

*Acacia drepanolobium* seeds were not found in any of the soil samples collected and examined for soil seed banks. Seeds recovered after sieving were mostly forbs, while seedlings that emerged from the germination trays were forbs, grasses, and seedlings of *A. brevispica* (especially from the red luvic arenosols). Because no *A. drepanolobium* seeds were recovered from these soils, no further analysis was done, and the soils were deemed to be devoid of *A. drepanolobium* seeds.

### 5.4.4 Germination and establishment of *Acacia drepanolobium*

#### *5.4.4.1 Influence of Hydrochloric acid on seed germination*

Acid treatment had no significant influence on the germination of *A. drepanolobium* seeds (F=0.02, P=0.88), (Table 5.1, Fig 5.1). However, acid-treated normal seeds germinated more quickly than the controls (Fig. 5.1). On average, control seeds took 35% (5.4 days) longer to germinate than scarified seeds (4.0 days). Burning and bruchid damage significantly reduced germination of *A. drepanolobium* seeds (F=85.11, P<0.001) compared with undamaged ones. Bruchid damaged seeds showed a very weak tendency (F=3.57, P=0.083) for a greater percent germination (10%) than burnt seeds (1.6%). Germination depended on the types of seed used (burnt, bruchid damaged or normal) (F=85.11, P<0.0001), with normal seeds having the greatest germination. This result showed that *A. drepanolobium* seeds do not need acid scarification or fire treatments for germination to occur. This result was used in designing the germination trials described in section 5.3.4.2.

Table 5.1 Mean percent germination (± S. E.) of three treatments of *A. drepanolobium* seeds with and without 1-M hydrochloric acid treatment. N = 60 seeds in each treatment combination, split into three replicates

| Seed type \ Treatment | Acid treated (%) | Control (%) |
|---|---|---|
| Bruchid damaged | 10.0 ± 0.00 | 10.0 ± 2.90 |
| Burnt | 3.3 ± 1.60 | 0.0 ± 0.00 |
| Normal (undamaged) | 73.0 ± 9.20 | 78.0 ± 4.40 |

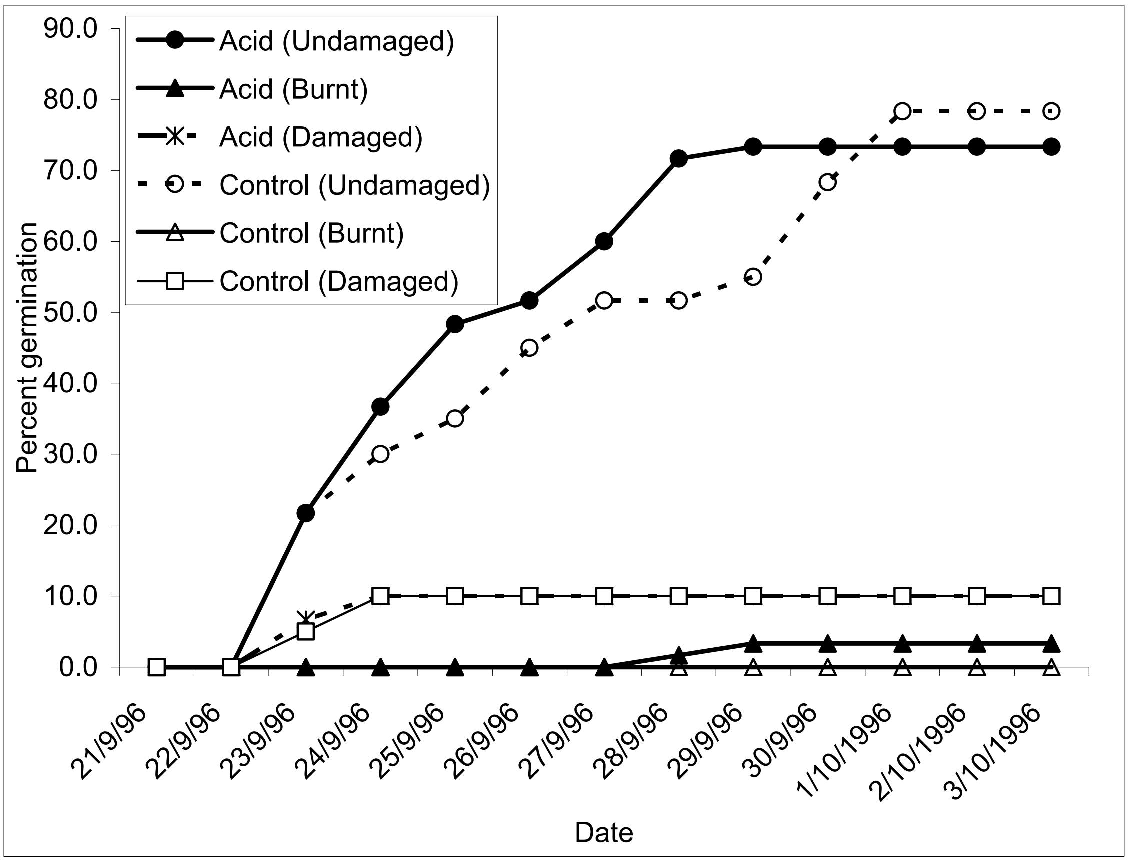

Fig. 5.1 Mean daily percent germination of burned, bruchid damaged and normal seeds of *A. drepanolobium* seeds with and without acid scarification.

### 5.4.5 Effects of seed and soil type on germination and seedling establishment

Germination and growth of *A. drepanolobium* seedlings were monitored for 19 weeks. There was no significant interaction between the seed treatments and soil type on seed germination and seedling establishment (F=0.57, P=0.69). Mean percent germination was different among the three seed treatments (F=112.5, P<0.001). Germination was greatest for undamaged seeds and lowest for burnt seeds (Table 5.2).

Table 5.2 Mean percent germination (± S.E.) of three treatments of *A. drepanolobium* seeds under different soil types. N = 147 in each treatment combination in three replicates of 49. Total number of seeds 1323

| Soil \ Seed type | Bruchid damaged (%) | Burnt (%) | Undamaged (%) |
|---|---|---|---|
| Red | 17.7 ± 4.1 | 5.4 ± 1.8 | 89.2 ± 2.4 |
| Loam | 15.6 ± 4.1 | 2.0 ± 1.2 | 77.5 ± 10.8 |
| Black | 28.7 ± 16.7 | 2.7 ± 1.4 | 86.4 ± 2.7 |
| Mean | 20.7 ± 4.1 | 3.4 ± 1.0 | 84.4 ± 3.5 |

These results are consistent with those from the pilot experiment above except that here, bruchid damaged seeds had a significantly higher percent germination compared to burnt seeds (F=8.91, P=0.008). Soil type did not influence seed germination (F=1.03, P = 0.378). Bruchid damaged seeds took an average of 8.0 days to germinate compared with 8.9 and 11.3 days for undamaged and burnt seeds respectively. Bruchid damaged seeds germinated significantly faster than burnt seeds (P = 0.048).

Growth rates of the three seed treatments were similar, (F=0.75, P= 0.567). By the 16th week, mean vertical growth was marginally higher in the loam soil (13.6 cm) compared with the black soil (13.1cm). Undamaged (control) seeds also showed marginally higher growth in all soil types up to the 16th week. Growth rate of seedlings from undamaged seeds was high at the beginning but began to decline after 12 weeks (Figs. 5.2; 5.3). The slowing down of growth rates of seedlings from this treatment was probably due to overcrowding and intense competition for nutrients. There was an average of 40 seedlings in an area of .025 $m^2$ (density of 1600 seedlings $m^{-2}$ for seedlings from undamaged seeds. During the course of growth, nutrients may be depleted, and this probably reduced growth rates.

Seedlings from burnt seeds had consistently slower growth compared with the other treatments, though the growth rates increased with time. By the 19th week, these seedlings were still growing at an increasing rate. This increase is probably due to the low seedling density and, therefore, less competition for nutrients. At the end of the 19th week, seedlings from the damaged seeds had an average height of 17.5 cm compared with 17.2 cm and 14.4 cm for burnt and undamaged seedlings respectively.

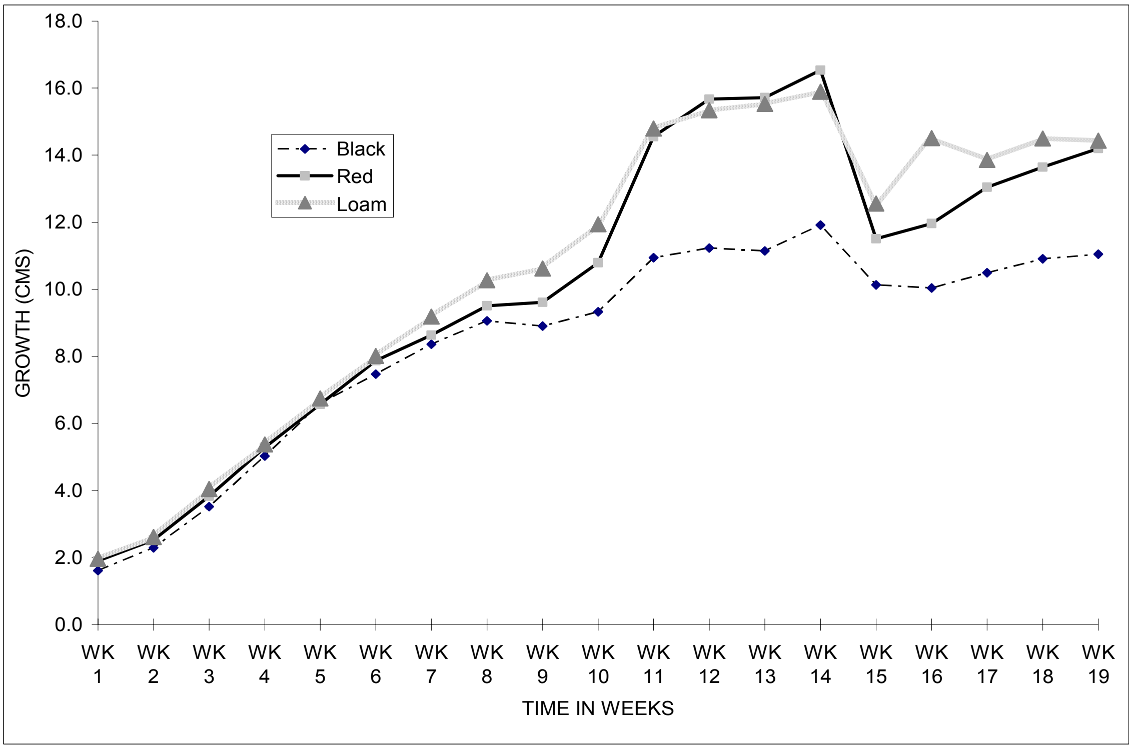

Fig. 5.2 Mean growth rate of *A. drepanolobium* seedlings in three soil types.

Seedling survival showed no differences among the three seed treatments (F=1.00, P<0.385) or soil types (F=2.44, P=0.115). There was no interaction between soil type and mortality (F=0.75, P=0.569), (Table 5.3). Seedlings from undamaged seeds on average survived longer (23 days) than those from burnt (18 days), or from bruchid damaged seeds (11 days).

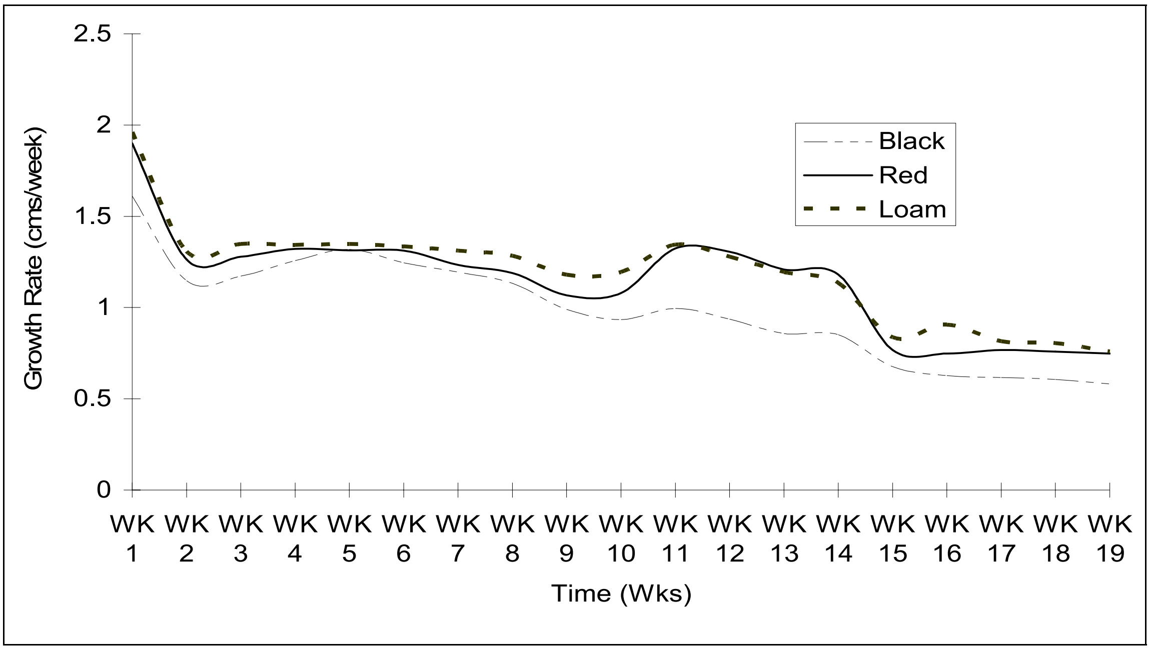

Fig. 5.3 Mean growth rate of *A. drepanolobium* seedlings in three soil types.

Table 5.3 Mean percent survival (± S.E.) of seedlings from three *A. drepanolobium* seed treatments under different soil types. n = 147 seeds in each treatment combination, in three replicates of 49. Total number of seeds 1323

| Soil \ Seed type | Bruchid damaged | Burnt | Undamaged |
|---|---|---|---|
| Red | 94.6 ± 2.9 | 99.3 ± 0.7 | 89.1 ± 3.8 |
| Loam | 91.8 ± 4.2 | 98.0 ± 1.2 | 86.4 ± 6.5 |
| Black Cotton | 77.5 ± 1.5 | 100.0 ± 0.0 | 91.8 ± 1.2 |
| Mean | 87.9 ± 5.3 | 99.1 ± 0.6 | 89.1 ± 1.6 |

### 5.4.6 Effect of fire on germination of *Acacia drepanolobium* seeds

Some seeds were not recovered after the fire experiment. A significantly greater number of buried seeds than surface placed seeds were recovered (F=78.4, P<0.001). Of those placed on the surface, an average of 33% was recovered, while 72% of those buried in the soil were recovered (Table 5.4). It was suspected that most of the seeds not recovered from the surface were either burned beyond recognition or were consumed by rodents, the mice *Saccostomus mearnsi* (Keesing 1998; 2000), being the prime suspect. It is also possible that birds predated some seeds. The loss of buried seeds was attributed solely to predation, possibly by rodents and other burrowing animals, because all the recovered seeds did not show any signs of burning.

Table 5.4 Relative and absolute percent germination of buried and surface placed *A. drepanolobium* seeds after a prescribed fire. Figures in parenthesis indicate the number of seeds recovered and used for germination trials after the fire. Percent relative germination is based on the number of recovered seeds only, while absolute germination is based on a sample of 100 seeds per treatment, 1000 seeds in total

| | | Screen house germination | Field germination |
|---|---|---|---|
| % Relative germination | Buried seeds | 37.2 (753) | 40.0 (677) |
| | Surface seeds | 2.0 (332) | 3.3 (337) |
| % Absolute germination | Buried seeds | 13.0 | 13.0 |
| | Surface seeds | 0.3 | 0.4 |

Germination was significantly greater for seeds that had been buried beneath the soil surface (F=151.2, P<0.0001) for both laboratory and field germination tests, than seeds placed on the surface (Table 6.5). Similar germination rates were achieved in both the field and in the laboratory (F=0.29, P=0.748). The observed difference in germination between surface placed and buried seeds was attributed the effect of fire on the seeds.

## 5.5 DISCUSSION

### 5.5.1 Flowering, pod and seed production

Flowering in the KLEE experiment and its immediate vicinity was negligible over a three-year period. So far, no plausible explanation has been suggested for this observation, and this phenomenon should be investigated further. Although factors that affect flowering and seed production were not directly investigated, *A. drepanolobium* populations in areas further from the KLEE flowered up to three times a year. In these areas, flowering started a few days before the rains actually fell. Many *Acacia* species flower before the rains (Ross 1979, Coe & Beentje 1991) and some authors have suggested that this is induced by moisture in the air. In the Laikipia rangelands, *A. nilotica* and *A. etbaica* also started flowering before rains actually fall. This phenomenon can be an adaptation to the variable rainfall in these environments.

The site from which pods were harvested had a mean density of 689 trees ha$^{-1}$, far less than the mean density of *A. drepanolobium* over a wide range, and *C. mimosae* was the resident ant in all trees (31) at this site. The relationship between seed production and tree height (95-205 cm) was weak for the *A. drepanolobium* surveyed. However, the variation in heights surveyed was small, and it is possible that seed production is greater for bigger trees.

Seed yield of 6.5 X 10$^{5}$ seeds ha$^{-1}$ for the studied site is probably the least that can be produced when *A. drepanolobium* trees flower, and is much lower than the 9.8 X 10$^{5}$ seeds ha$^{-1}$ reported for *A. sieberiana* in Uganda (Mucunguzi 1995). The yields are assumed to be low because, (i) the trees surveyed were small, and (ii) *A. drepanolobium* can flower more than once a year. If seed production is strongly correlated with tree size, then seed production in *A. drepanolobium* would be expected to be quite high, and together with the high germination rates, portends encroachment, especially if most of the seeds are viable. Enough seeds are probably produced to satiate most of the predators as well.

Flowering and seed production of *A. drepanolobium* displayed spatial and temporal variation and patchiness. Less than 2% of 1800 tagged trees had shown any flowering over a three year period, while stands less than 2 km away, on similar soils, rainfall, altitude and management flowered and produced seeds profusely every year.

A question that arises from the observed flowering patterns is whether seed availability is likely to be a constraint on increasing population size? With respect to the spatial pattern of flowering, it would be important to know the factors that contribute to it.

### 5.5.2 Bruchid infestation and seed depredation

Bruchid infestation of *Acacia* species has been widely reported e.g. (Miller & Coe 1993) and the range of infested seeds is wide, (Mucunguzi 1995). In this study, only *Bruchus* sp. was found in *A. drepanolobium* seeds. The bruchid beetles attacked between 30 and 100% of the seeds, indicating that bruchid beetles are very important in the population dynamics of this tree, since the beetles significantly suppress the germination of seeds (see section below).

There are other predators of *A. drepanolobium* seeds. Keesing (1998, 2000) reported that the pouched mouse (*Saccostomus mearnsi*) consumed about 93 % of seeds on offer. The mice are suspected of predating seeds of *A. drepanolobium* on the surface and those buried in the soil. Birds also predated on the seeds of *A. drepanolobium*. Whole pods of *A. drepanolobium* were also found in elephant dung. All the herbivores that feed on *A. drepanolobium* e.g. eland, giraffe and hartebeest, were also suspected of eating *A. drepanolobium* seeds since they browsed the pods. The findings suggest that smaller herbivores (e.g. goats and Grant's gazelle) completely crush and probably digest the seeds, while some seeds may escape mastication by larger mammals.

Many African *Acacia* species have been reported to have many predators e.g. herbivores (Miller 1994b), but predation of *Acacia* seeds may not limit its regeneration from seed because *Acacia* species produce large quantities of seeds that may lead to predator satiation (Halevy 1974, Lamprey 1974). The high germination rates found in this species suggest that only a few seeds need to escape from predation to germinate.

If some *A. drepanolobium* seeds escape digestion by goats, Grant's gazelle, eland and hartebeest, then these herbivores may play an important role in its dispersal and therefore encroachment. However, *A. drepanolobium* is among the least preferred of the browse species at Mpala because of the belligerent ants (chapter 4), and its consumption is therefore low, implying that herbivores may not play a very important role in its dispersal. Moreover, seeds were only recovered from elephant dung. On the other hand, smaller herbivores e.g. goats and Grant's gazelles may not be useful as dispersal agents since they crush (or digest) the seeds (Belsky 1984).

### 5.5.3 Effects of bruchid beetles, fire and soil type on the germination and seedling establishment of *Acacia drepanolobium*

The ability of a species to replace itself is of major ecological and economic importance (Cavanagh 1980). Germination and early growth are the critical phases in the population dynamics of *Acacia* species (Halevy 1974; Fenner 1986). These processes determine the density and distribution of *Acacia* species (Oba 1990), owing to the high mortality that characterize them (Coe & Coe 1987).

*A. drepanolobium* seeds do not need scarification or pre-sowing seed treatments to germinate. This is consistent with the widely held view that seeds of dehiscent acacias germinate readily without need for scarification (Lamprey 1974). In the pilot study, both scarified and non-scarified seeds gave similar rates of germination. However, the scarified seeds required less time to reach peak germination compared with the control.

Bruchid-damaged seeds also took marginally less time to germinate compared with undamaged and burnt seeds. The time differences recorded in both the pilot and main experiment were, however, small, and may not be important in field germination. This result suggests that acid-treated and bruchid-damaged seeds may respond marginally faster to appropriate conditions for germination than the other seed types. This may be important in habitats where appropriate conditions for germination are short lived.

Bruchid beetles that feed on *A. drepanolobium* seeds significantly limit their germination potential. Seeds that germinate may not have enough reserves to survive competition and establish. Percent germination of damaged seeds in this study was much lower than the control. The higher mortality recorded in the seedlings from bruchid damaged seeds suggest that the seedlings may be weak as a result of depleted food reserves during early growth due to infestation by the *Bruchus* sp. which consumes quite a substantial portion of the seed food reserves.

Bruchid larvae are predators of the seed reserves and can therefore influence the germination rate of *Acacia* seeds (Halevy 1974; Lamprey *et al.* 1974; Miller 1994c; Miller 1995). Though Lamprey *et al.* (1974) and Halevy (1974) suggested that the holes created by the bruchid larvae enhance permeability of the seed testa, and hence, have a positive effect on *Acacia* seed germination, Miller (1994b; 1995) and Mucunguzi (1995) reported no difference in germination rates between bruchid damaged and undamaged seeds of *A. nilotica, A. tortilis*, and A. *hebeclada*. All these species are indehiscent species.

Lamprey *et al.* (1974); Mucunguzi (1995); and Halevy (1974), reported 6% germination in bruchid-damaged seeds of *A. gerardii,* a dehiscent species. Germination of bruchid-damaged seeds in this study was 10-20% higher. Mucunguzi (1995) concluded that bruchid beetles promoted early germination and establishment of *A. sieberiana.* He recorded 17% germination in bruchid-damaged seeds, and no germination in undamaged seeds, yet when the undamaged seeds were pre-treated with 1M HCL., germination reached 80%.

Earlier workers like Halevy (1974), and Lamprey (1974) thought that the exit holes of adult bruchid beetles were used for water imbibition. But recent evidence by Miller (1994a, b, c) suggests that seeds with exit holes are in most cases unviable since most of the food reserves have been consumed, and water primarily enters the seeds via the larval entry holes. Most of the seeds that had been attacked by bruchid beetles in this study had most of the seed contents eaten up, suggesting that the seeds were probably dead, and could not germinate. In general, bruchid damage adversely influences germinability of most *Acacia* seeds (Mucunguzi 1995) though not exclusively so. The cost of bruchid damage, which results in reduced seed viability potential, may be compensated by the production of large numbers of seeds (Halevy 1974; Lamprey 1974). Survival was much lower, though not significantly so, in seedlings from damaged seeds compared to those from undamaged and burnt seeds.

Both germination trials recorded marginal rates of germination for burnt seeds. Hodgkinson & Oxley (1990) argued that fire promotes germination for some species by the action of its heat, which opens the lens behind the helium, an act that allows in water and results in germination. Coe & Coe (1987) postulated that fire events in the savanna were likely to be a means of increasing water permeability of the testa.

However, high fire temperatures kill seeds. For example, Hodgkinson & Oxley (1990) reported that seeds of *Acacia aneura* were killed at fire temperatures exceeding 80°C. There seems to be a threshold temperature beyond which fire kills seeds, but this is species specific (Ramsey & Oxley 1996). Cavanagh (1980) reported that *Acacia* seeds could withstand prolonged periods of exposure to dry, but not to moist heat. They found most seeds dead at temperatures of 110 – 120° C when exposed for short periods.

Despite its reported effects on seed germination, fire is not a pre-requisite for field germination (Cavanagh 1980), and this has been confirmed in this study where germination from control seeds was quite high. Fire temperatures recorded in the field (chapter 6) averaged 230 °C at the ground level, and it may have been beyond the threshold level for *A. drepanolobium* and, indeed, for most *Acacia* species (Ramsey & Oxley 1996; Cavanagh 1980).

The present findings suggest that fire can be an important tool in the management of *A. drepanolobium* regeneration from seed. Fire may stifle germination of new seeds by killing them, thereby significantly limiting recruitment of new seedlings. This has important consequences in the population dynamics of *Acacia* species, which mostly regenerate from seed to effectively propagate (Harper 1977). Burnt seeds also took slightly longer to germinate than the other two treatments, while bruchid damaged seeds took a shorter time to germinate. This implies that burnt seeds may not exploit the short windows conducive for germination in harsh habitats.

Throughout East Africa, *A. drepanolobium* is largely restricted to black cotton and similar heavy clays with impeded drainage, where it forms a virtual mono-culture. In central Laikipia, this soil restriction is abrupt and complete. Two alternative hypotheses are possible. First, *A. drepanolobium* may be unable to germinate, establish and grow on soils other than black cotton soils. Second, *A. drepanolobium* may be uniquely adapted to these specialised soils, and although it can grow on alternative soils in green house conditions, it is at a competitive disadvantage in such soils by other tree and shrub species from which it is excluded.

These results provide empirical evidence that the alternative major soil type, in Laikipia does not restrict the germination or establishment of *A. drepanolobium*. While it remains possible that such a restriction occurs at a later life stage, this is unlikely. Although *A. drepanolobium* are not found beyond the narrow ecotone of black cotton soil types in Laikipia, it is more likely that the restriction to black cotton soils is related to the competitive conditions in alternative communities. In fact, elsewhere in East Africa (and even Laikipia), *A. drepanolobium* can sometimes be found in other soil types (personal observation). However, it is not known why it is absent from large areas of red sandy soils in Laikipia. One possibility is that it is a poor competitor off black cotton soils.

This study has also shown that both fire and *Bruchus* sp. significantly limit regeneration *of A. drepanolobium* from seed. While *Bruchus* species can also enhances mortality of seedlings during early periods of establishment, fire can kill its seeds.

# 6 CHAPTER SIX: EFFECT OF FIRE ON *ACACIA DREPANOLOBIUM* WOODLAND

## 6.1 INTRODUCTION

Fires have historically been an important ecological occurrence in East African grassland and savanna ecosystems. They have influenced herbaceous composition, forage quality and density of woody species (Pratt & Gwynne 1977) that in turn has influenced wildlife dynamics and livestock production (Herlocker 1999).

Fires have been equally important in other grassland systems in southern Africa (Trollope 1981; O'Connor 1985; O'Connor & Everson 2000), the Mediterranean (Noy-Meir 1995), and North America (Humprey 1962; Bock *et al.*, 1995). In East Africa, fires were common in these ecosystems until the late 1950's (Heady 1978). However, fires have become more infrequent in ranching areas (e.g. in the Laikipia rangelands) in the last three decades because many ranchers consider them to be 'environmentally inappropriate' for range management (Mwihuri 1998). The decline in fire frequency, coupled with a reduction in the abundance of browsing herbivores, has apparently resulted in an increase of woody vegetation in the Laikipia ranching region (Okello 1996).

The effects of fire on African savanna are not well understood (Gichohi *et al*. 1996), such that the desired objectives of the use of fire are often not achieved (Wein & Edroma 1985). Similarly, the interactions of fire with climate, soil and herbivory are poorly understood (Hobbs & Grimmingham 1987; Bock *et al.* 1995; Whelan 1995).

In the Kiboko rangelands of southern Kenya, Tchie & Gakahu (1989) reported that a prescribed fire killed most plants of all browse species irrespective of height, while Oba (1990) reported that fire not only killed mature trees of *A. tortilis* in the Turkwel valley of north western Kenya, but also resulted in high germination of *A. tortilis* seeds. In the savannas, it is to be expected that fire would have a greater impact on seedlings and small trees and shrubs than on mature trees (Pellew 1983). Some tree and shrub species have adapted well to savanna fires (Oba 1990), the adaptations taking various forms for example, coppicing (Sabiiti & Wein 1988), thick bark (Oba 1990), and prolific germination and growth of seedlings (Sabiiti & Wein 1987).

*Acacia drepanolobium*, the dominant woody species over large areas of Laikipia plateau on soils with impeded drainage (Young *et al*. 1998), has increased in density and expanded its range in the last 30 to 40 years (Jacky Kenyon 1996[5], pers. comm.). A reduction in fire frequency has also altered the composition of the herbaceous layer from a sward dominated by *Themeda triandra*, a species commonly considered to thrive under fire (Edroma 1984; O'Connor 1985; Morris *et al*. 1992), to one dominated by *Pennisetum stramineum* and *P. mezianum* (Okello 1996; Mwihuri 1998). The response of the latter two species to fire is unknown.

Many ranch managers in Laikipia are increasingly harvesting grass for use as hay during dry spells (pers. observation), an action whose effects on the herb layer species composition and forage quality is not known. In some grasslands, mowing had a direct effect on species composition and cover (Tainton *et al.* 1977; Le Roux & Morris 1977; Morris *et al.* 1992). Tainton *et al*. (1977) and Dorgelow (1999) reported that burning and mowing may influence the forage value of range grasses. Nutritional value of vegetation is usually measured by digestibility, crude protein and mineral availability (Shackleton & Mentis 1992).

In practical range management, the desired goal is to have herb layer species with high forage value, but the effect of fire on herbaceous composition and forage quality of the grasslands of Laikipia is unknown.

High density of trees often leads to a decline in grassland productivity (O'Connor 1985). In areas of Laikipia with a dense cover of *A. drepanolobium*, little grass is found under its canopy, a cause of concern to managers. Many attempts have been made to control *A. drepanolobium* including chemicals (Outrum 1970), physical clearing and fire (Pratt & Knight 1971). However, effects of fire on *A. drepanolobium* and other co-occurring species are unclear. Results in chapter five indicate that fire killed *A. drepanolobium* seeds thus limiting their regeneration from seed, and this phenomenon could be used as a first step for controlling it.

## 6.2 OBJECTIVES OF INVESTIGATION

This chapter aims at quantifying the effects of fire on the demography of *A. drepanolobium* and herb layer species composition and cover for managing woodlands. The experiment

---

[5] Jack Kenyon, Mogwooni Ranch, P O. Box 248 Nanyuki, Kenya.

was conducted to test the effect of fire on the population dynamics of *A. drepanolobium* and its relevance to the proper management of the Laikipia rangelands. The specific objectives were:

1. To investigate the effects of fire on the demography *of A. drepanolobium;* and
2. Document changes in the herb layer species composition and cover before and after a fire and mowing.

## 6.3 MATERIALS AND METHODS

### 6.3.1 Study area and site

A description of the study was presented in chapter three. (See also Appendix 1 for further details). The study site for this experiment was half a kilometre to the north of the KLEE site, but with similar climate, soils and vegetation (Fig. 3.1). Overstorey vegetation is dominated by *A. drepanolobium*, which *accounts* for 88-97% of the trees and shrubs (Young *et al.* 1998). Other tree and shrub species are *Rhus natalensis, Grewia similis, G. bicolor*, and *Cadaba farinosa*. *Pennisetum mezianum*, *P. stramineum*, *Themeda triandra*, *Lintonia nutans*, and *Brachiaria brizantha* dominate the herb layer. Other herb-layer species include *Bothriochloa insculpta* and *Indigofera spinosa.*

### 6.3.2 The fire experiment

A burning experiment was designed to study the response of *A. drepanolobium* and the herb layer species to fire. The experimental design entailed burning three five-hectare plots (500 by 100m). However, only one experimental plot was available for the study because of management restrictions. It is acknowledged that a major shortcoming of this experiment was the lack of replication of the fire and mowing treatments.

The experiment would have had greater power of inference and more precise interpretation had it been replicated. The large size of the experimental plots justifies the results obtained. The area burnt was uniform (slope, soil, vegetation, species composition and past and present use), and considered large enough. The five-hectare burn-plot was bounded on two sides by graded tracks, and a 3 m wide firebreak was graded around the remaining sides.

A 10 by 100-m strip was mowed on the western side of the site to further widen the firebreak. This strip provided a unique opportunity for comparing herb layer floristic composition, cover, flowering of mowed, burned, and unburned plots. Although this strip had been mowed before, its history of mowing is not known.

Tempilstik® crayons were used to monitor fire temperatures. These crayons melt and change colour when their marked temperatures are reached. Seven Tempilstik® temperature markers that melt at 66 $^{o}$C, 124 $^{o}$C, 149 $^{o}$C, 204 $^{o}$C, 302 $^{o}$C, and 500 $^{o}$C, were painted on asbestos slabs of 20 cm X 15 cm in area. These asbestos slabs were placed at ten stations, 50 m apart, at each of four height levels, ground level, 50 cm, 150 cm and 300 cm above the ground.

Temperature markers for the last three heights were nailed on *A. drepanolobium* trees. Locating the measuring stations at a tree was considered acceptable in view of the objectives of the study. The first and last fire temperature stations were located 50m inside the burn plot from either end.

Air temperature and humidity were monitored by a thermohygrograph from a mini-weather station located 100-m from the burn plot. Wind speed was monitored using an anemometer mounted on a vehicle by the firebreak and recorded every ten minutes. The speed and height of the head fire were visually estimated at 10 stations, 50 m apart along the side of the burn plot. Five of these stations corresponded with the temperature stations.

Before burning, 30 quadrats, each 0.25 $m^2$ in area, of herbaceous material were randomly selected and clipped to determine the fuel load. The clipped material was oven-dried at 70 $^oC$ for 24 hours and weighed to the nearest 0.005g.

The fire was lit on 24th March 1998 at 12.24 p.m. and the plot had burned by 1.34 p.m. As a safety precaution, a 20-m back-burn from the south-western corner was first done then a head fire was started from the windward side.

### 6.3.3 Effect of fire on trees and shrubs

To monitor the survival of *A. drepanolobium* trees after a fire, overstorey species composition and density were estimated using 10 (5 m by 50 m) belt transects randomly located within the plot before the burn in March 1998, and re-sampled four months after the fire in July 1998. All trees and shrubs were identified and their heights measured to the nearest 1 cm. One hundred *A. drepanolobium* trees in four height-classes were tagged with numbered aluminium labels within the burn plot for post-fire monitoring. The height classes were 0-80 cm, 81 cm – 150 cm, 151 cm – 300 cm, and > 300 cm. The height and stem diameter at 25 cm above the ground of each tagged tree was measured before and a day after the fire. The fate of each tagged individual was monitored four months later in July 1998 and again in December 1998.

An index of tree damage was used to categorise the effect of fire on the trees: 1. 75% to 100% - top burn; 2. 50% to 75% burned; 3. 25% to 50% burned; 4 up to 25% burned; and 5. No apparent fire damage. The height at which the flame visibly burned the tree (indicated by the change in colour of leaves) was also recorded. Four months after the fire (July 1998), the tagged trees were measured for growth in height and stem diameters, and the number of coppicing stems per tree was recorded. However, some aluminium tags were removed from trees by animals (monkeys and baboons), thereby reducing the sample size by over 30%. The tree was treated as the experimental unit, fire the treatment, and the number of trees within the height classes were considered the replicates. The pseudo-replication within the experiment is acknowledged, this could not be avoided for lack of sites to replicate it. Transects were used as replicates for evaluation of the herb layer.

### 6.3.4 Effect of fire and mowing on herb layer species composition, foliage cover and nutrient quality

To evaluate herb layer species composition and cover within the burn plot, a 10-point pin frame (Bonham 1989) was placed eight times along the centre line of each belt transect. All hits by a pin were recorded for species composition, only the first hit was used to estimate cover. Subsequent herb layer measurements were done from the same spot within the belt transects. The nearby unburned and mowed plots were similarly inventoried for species richness and cover.

In August 1998 (five months after the burn), most of the grasses were flowering in all three treatments. An inventory to estimate species composition, cover, and flowering was done in each of the three treatments as stated above. All hits by a pin were recorded and used for estimating species composition and flowering, while the first hit was used to estimate canopy cover. Shannon-Weiner diversity index (Brower *et al*. 1990) was used to compare species diversity in the three treatments.

### 6.3.5 Data analysis

Correlation analysis (JMP-IN, SAS 1999) was used to analyse the patterns of horizontal and vertical temperature profiles.

Differences in relative cover by the major species were analysed by Model 1 ANOVA, (Steel & Torrie 1980).

## 6.4 RESULTS

### 6.4.1 Fire temperatures

Pre-fire fuel load within the burned plot was 8.7 ± 0.53 tonnes per ha of dry matter (11.8 ± 0.78 tonnes per ha wet weight, moisture 26.3%). The fire took about 70 minutes to burn the 5 ha plot. Dead wood smouldered on for at least 24 hours after the last flames had died out. Wind direction was north-easterly, and wind-speed ranged from 0.56 – 3.33 m $s^{-1}$, (mean 2.08 ± 0.36 m $s^{-1}$). Mean air temperature during the burning was 23 °C, and the humidity was 33%. Fire intensity was estimated using the multiple regression equation of Trollope & Trollope (2002), $FI = 2729 + 0.8684x_1 - 530\sqrt{x_2} - 0.907x_3^2 - 596\ 1/x_4$. Where

FI – fire intensity (kJ/s/m)
$X_1$ – fuel load (kg/ha)
$X_2$ – fuel moisture (%)
$X_3$ – relative humidity (%)
$X_4$ – wind speed (m/s)

The mean fire intensity based on the fire behaviour data was 8,642.92 kJ/s/m, which is quite high but within the range recorded for Southern and East African savannas (Trollope & Trollope 2002).

The amount of fuel available for burning was high, suggesting an accumulation of biomass over the years and that the herbage was probably not palatable to the large biomass of herbivores, or the herbivores were too few to significantly reduce it.

Maximum temperatures of more than 500 °C and minimum of 66 °C were attained at the ground surface and 300 cm height respectively (Fig. 6.1). Temperatures were higher at the ground level averaging 302.4 °C, and lowest at the 300 cm height (T= 92.8 °C). The vertical mean temperature (averaged over the 4 heights) was 170 ± 14 °C, ranging from 121 °C to 257 °C.

The temperature profile (Fig. 6.1) indicates that fire was not uniform over the burn plot. Temperature fluctuations were more prominent at stations on the ground and 50 cm levels compared with those at 150 cm and 300 cm high.

Correlation analysis showed weak relationships between temperature at the ground level and 300 cm high ($R^2 = 0.56$, $P = 0.09$), and between 50 cm height and those at 150 cm and 300 cm high ($R^2 = 0.42$, $P = 0.22$; and $R^2 = 0.33$, $P = 0.34$ respectively). Fluctuations at the ground level were of a higher magnitude (204 °C to 500 °C), compared with the 50 cm height (124 °C to 302 °C). Temperatures at the 150 cm and 300 cm heights were similar and did not fluctuate much ($R^2 = 0.78$, $P = 0.007$).

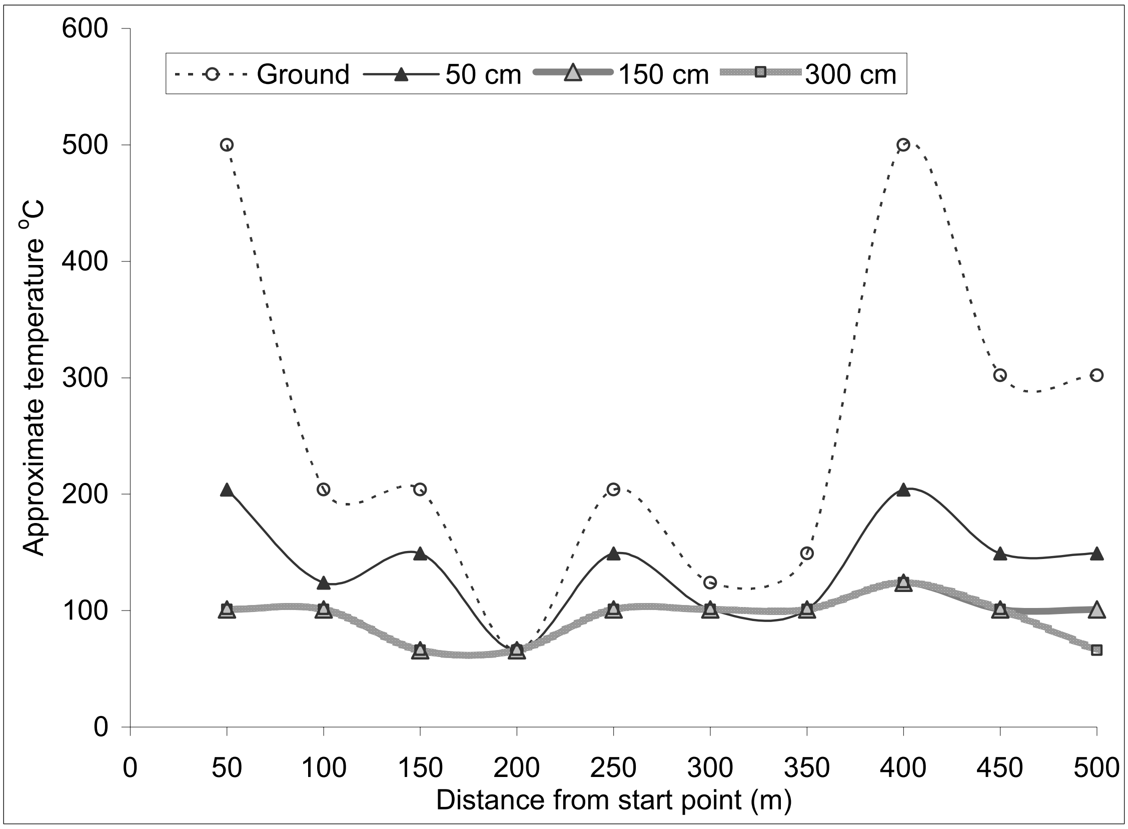

Fig. 6.1 Fire temperature profile showing horizontal and vertical changes in temperature at different points. Horizontal points are spaced at 50-m intervals; vertical points are located at ground level, 50 cm, 150 cm and 300 cm.

The flame height of the head fire also fluctuated with distance. Maximum flame height recorded was 400 cm, and minimum was 110 cm, indicating that almost all trees less than 100 cm tall probably experienced a top burn. Spots of unburned grasses remained, especially around *Lycium europaeum* and *Cadaba farinosa* bushes indicating that some bushes probably escaped the hot fires. However, they were most likely scorched by the heat.

A significant observation on the day after the fire was the large biomass of herbivores eating on burned wood and ash. Herbivores seen included giraffe, eland, hartebeest, zebra, Grant's gazelle, Thomson's gazelle and oryx. Elephants were conspicuously absent. Many birds were also attracted to the burnt site. Though estimates of dung droppings were made after the fire, this could not be compared with dung in the mowed or control plots because (i), the burn plot was sandwiched between the mowed and control plots, therefore all herbivores must have passed through either of these to reach the burn plot, hence any dung found in these plots would probably have been due to animals accessing the burn plot, and not intending to graze either the unburned or mowed plots. (ii), the control plot was very dense with grasses, most of which were at least 100 cm tall, and therefore seeing or identifying the dung would have been prone to error.

### 6.4.2 Fire effect on tree density and composition

Pre- and post-fire tree and shrub density were 904 and 870 trees per hectare respectively, a post-fire loss of about 3%. *Acacia drepanolobium* was the main overstorey species, accounting for 89.4% and 96.1% of the overstorey species before and after the fire respectively (Table 6.1). The size class distribution did not follow a clustered reverse J-shape like in the KLEE experiment (chapter 4, Fig 4.1). The number of small trees (less than 80 cm in height) was low contributing only 7% of the total tree density, suggesting poor recruitment of seedlings since this site had a lower density than the KLEE site.

Table 6.1 Percent overstorey species composition and density (trees per hectare) before and after a prescribed fire in an *Acacia drepanolobium* wooded grassland at Mpala

| | Pre-fire March 1998 | | Post-fire March 1998 | | Post-fire December 1998 | |
|---|---|---|---|---|---|---|
| Species | Density | Composition | Density | Composition | Density | Composition |
| *A. drepanolobium* | 808 | 89.4 | 804 | 92.4 | 808 | 96.1 |
| *Rhus natalensis* | 40 | 4.4 | 32 | 3.7 | 20 | 2.4 |
| *Cadaba farinosa* | 24 | 2.7 | 20 | 2.3 | 8 | 0.9 |
| *L. europaeum* | 24 | 2.7 | 8 | 0.9 | 0 | 0.0 |
| *Grewia* sp. | 8 | 0.8 | 6 | 0.7 | 5 | 0.6 |
| Total | 904 | | 870 | | 841 | 100.0 |

*Acacia drepanolobium* trees did not succumb to the fire, and no tree died because of burning. Small trees only died back, but were not completely eliminated by the fire. About 16% of *A. drepanolobium* trees were top-killed (Table 6.2), but by December 1998, all the top-killed *A. drepanolobium* trees were alive and at various stages of coppicing

The impact of fire was greater on shorter than on taller trees of *A. drepanolobium*. This implies that a trees' reaction to fire (e.g. growth and mortality), would probably be in the same direction, inverse to tree height.

Table 6.2 Qualitative index of fire damage on *A. drepanolobium* trees in different size classes expressed on a percent basis

| | Index of fire damage | | | | |
|---|---|---|---|---|---|
| Height class | 1 | 2 | 3 | 4 | 5 |
| < 80 cm | 16.7 | 50.0 | 27.8 | 5.6 | 0 |
| 80 cm – 150 cm | 8.0 | 28.0 | 52.0 | 12.0 | 0 |
| 151 cm –300 cm | 5.4 | 16.1 | 64.3 | 14.3 | 0 |
| > 300 cm | 0 | 5.5 | 43.6 | 40.0 | 10.9 |

Legend: 1- 100 % top killed, 2- 50 to 75% burnt, 3- 25 to 50% burnt, 4- 25% burnt, 5 - no damage noticed.

Fire damage index 2 is severe enough to affect the physiological functioning of the tree that may lead to reallocation of the tree's resources. Though the index of fire damage does not show to what extent a tree was harmed, it is a useful guide of the harm to a tree by fire. In particular, the index of damage in this experiment is consistent with the expectation that smaller trees would be more susceptible to fire damage than larger trees.

Among the other woody species, densities of *Grewia* sp., *Cadaba farinosa, Rhus natalensis,* and *Lycium europaeum* were reduced by between 50% and 100% of their pre-fire densities (Table 6.1). The immediate post fire (March 1998) estimates showed only mild losses, of between 20% and 66% for the other tree and shrub species. Density and species composition estimates done in December 1998 indicated that higher mortality had taken place in these species. This indicates that the effect of fire on survival or mortality may not be apparent immediately after a fire. It is possible that factors other than fire may contribute to mortality, especially after fire has weakened trees.

None of the other species that were burned showed signs of coppicing. In fact, all *Grewia sp., Cadaba farinosa, Rhus natalensis,* and *Lycium europium* died months after the fire, despite the fact that fire did not entirely consume them during the burn. None had shown any signs of regeneration from seed either by December 1998, suggesting that they are sensitive to fires, at least of the kind that burned them. Since most of the other woody species were less than 200 cm in height, it can be assumed that they experienced a fire damage of index 2, and despite some escaping from the hot fire itself, most were scorched.

### 6.4.3 Coppicing and growth of *Acacia drepanolobium* after fire

#### ***6.4.3.1 Coppicing after burning***

The most visible reaction of *A. drepanolobium* to fire was coppicing after the first rains. *Acacia drepanolobium* trees up to 300 cm tall coppiced mainly from the base of the stems.

Coppicing was greatest in the 80 cm to 150 cm height class (Table 6.3). The trend of coppicing was consistent with the observed trend in the index of fire damage, with smaller trees that were more affected with the fire having significantly more coppice stems compared with bigger trees, which were not as affected by the fire (F=5.27, P=0.0024).

Coppicing normally takes place when stems from a tree are dead or rendered non-functional. The coppicing material then becomes the living part of the plant above the ground. The mean number of coppice stems per individual tree was three and showed an inverse trend with increasing tree height (Table 6.3)

Table 6.3 Percentage of *A. drepanolobium* trees coppicing, the mean number of coppice per plant, and mean lengths of the two longest coppicing stems based on height classes in the burnt plot

| Height Class (cm) | % Coppicing | Mean number of coppice | Mean coppice lengths (cm) | |
|---|---|---|---|---|
| | | | Longest stem | 2nd longest Stem |
| < 80 | 37.5 | 3.3 | 14.12 | 8.62 |
| 81 -150 | 75.0 | 3.2 | 26.92 | 17.83 |
| 150 -300 | 31.8 | 2.6 | 15.08 | 10.5 |
| > 300 | 0.0 | 0.0 | - | - |

Results in chapter 7 indicate that the number of coppicing stems decline with time, indicating that some coppice stems are shed off probably as apical dominance asserts itself. Trees greater than 300 cm did not coppice at all, because none of their stems were wholly consumed or damaged by fire, and were still functional. This may be attributed to the lower fire damage index (3-5) in this class.

#### *6.4.3.2 Growth of Acacia drepanolobium after burning*

After five months and 391 mm of rain, *A. drepanolobium* trees in the 150 cm – 300 cm height class showed the greatest mean increase in height of 14.9 cm (35.8 cm per annum), which is higher than the mean annual growth in height reported for *A. drepanolobium* (24.5 cm) in chapter four, as well as for the other height classes in this experiment (Table 6.4).

Table 6.4 Growth in height and diameter of *A. drepanolobium* five months after a fire in the burnt plots. Sample size was reduced due to loss of tagged trees

| Height class (cm) | Height growth (cm) | Diameter growth (mm) | Number of trees |
|---|---|---|---|
| < 80 | 4.9 ± 9.19 | 27.5 ± 14.1 | 8 |
| 81 cm-150 | -3.9 ± 8.20 | 3.3 ± 1.33 | 12 |
| 150 cm-300 | 14.9 ± 2.32 | 7.1 ± 2.51 | 24 |
| > 300 | 5.3 ± 10.60 | 31.1 ± 9.69 | 20 |

Trees in the 81 cm – 150 cm height class recorded an average decline in height, yet they had the greatest growth of coppice. This was attributed to fire consuming part of the crown, which later fell off in some trees, or the reallocation of resources to coppicing in others. The biggest height class (>300 cm) had the greatest increase in basal diameter of 3.1 cm, while the 81 cm to 150 cm height class had the least (0.33 cm) increase in girth. This increase in girth is also higher than that reported in chapter 4. The growth patterns of *A. drepanolobium* reported here indicate that fire probably contributed to the growth by way of releasing certain minerals like nitrogen and phosphorus to the plants from either woody material, or those locked up in the soil and grass.

### 6.4.4 Effect of fire and mowing on species composition and cover of the herb layer

The main herb layer species found in the study sites before the burn were grasses that had a mean foliage cover of 94.7%. *Themeda triandra*, *Pennisetum stramineum*, *P. mezianum*, *Lintonia nutans*, and *Brachiaria brizantha* were dominant (Table 6.5). *Themeda triandra* is an erect bunch grass of great value to grazing (Edroma 1984) and is often sensitive to grazing (Pratt *et al.* 1966; O'Connor 1985; O'Connor & Everson 2000). *Pennisetum stramineum* and *P. mezianum* are rhizomatous grasses that are grazing resistant or tolerant (Bogdan 1958), while *L. nutans* and *B. brizantha* are stoloniferous grasses. *Lintonia nutans* is regarded as being of little grazing value, while *B. brizantha* is of high grazing value (Bogdan 1958).

Both fire and mowing treatments did not affect foliage cover (F=0.20, P=0.96) although there was a general decrease in percent foliage cover after the treatments. However, relative foliage cover by individual major species differed after the burn (F=13.39, P=0.0001).

Table 6.5 Relative contribution to percent cover of the main herbaceous species before and 3 months after a day fire in *Acacia drepanolobium* savanna

| | Before fire (March 1998) | | | After fire (June 1998) | | |
|---|---|---|---|---|---|---|
| Species | Unburned | Burnt | Mowed | Unburned | Burnt | Mowed |
| *Brachiaria brizantha* | 13.3 | 15.3 | 2.8 | 12.0 | 12.1 | 0.0 |
| *Lintonia nutans* | 6.3 | 8.0 | 28.8 | 6.8 | 6.0 | 49.0 |
| *Pennisetum mezianum* | 26.0 | 24.4 | 20.1 | 25.9 | 14.5 | 19.9 |
| *P. stramineum* | 8.0 | 8.9 | 11.4 | 7.9 | 12.5 | 7.3 |
| *Themeda triandra* | 34.0 | 29.3 | 16.7 | 34.1 | 25.8 | 4.3 |
| Others | 7.3 | 8.8 | 8.0 | 7.5 | 14.8 | 5.1 |
| Bare ground | 5.1 | 5.3 | 12.2 | 5.8 | 14.3 | 14.5 |

The percent bare ground more than doubled after the fire. Both burned (83.3%) and mowed plots (85.4%) recorded lower foliage cover than the unburned (94.4%) plot. Herb layer species composition did not change much after the fire (Table 6.6).

Four new species, *Digitaria velutina, Indigofera spinosa, Ipomea* sp., and *Leucas* sp. were recorded for the first time, while *Cenchrus ciliaris, Aristida* sp., *Commelina africana* and *Barleria* sp. were not present after the fire. Despite these changes in composition, diversity as measured by Shannon-Weiner index remained the same (H’ = 0.81) before and after the fire.

### 6.4.5 Effect of fire and mowing on the flowering of the major grass species

Mean percent flowering was different among the three treatments (F=12.57, P=0.0001) being generally greatest in the mowed and least in the unburned treatments respectively (Fig 6.2). Species also differed in the mean percent flowering in each of the treatments (F=14.71, P=0.0001). *Themeda triandra* had the greatest mean percent flowering in the burned and unburned treatments, but its flowering was significantly greater in the burned plot. In the mowed plot, *L. nutans* had the greatest flowering. These results suggest that fire and mowing enhanced flowering in *T. triandra* and *L. nutans* respectively.

Mowing enhanced flowering in all the five major species except *B. brizantha* (Fig. 6.2). The mowed plot had the greatest flowering (38.8%), double that in the burned (15.2%), and five times that in the unburned plot. *Themeda triandra* contributed most to flowering in the burned plot, while *Lintonia nutans* contributed most to flowering in the mowed plot. Fire and mowing seem to have suppressed flowering in the less common species, which recorded 12.8% and 8.7% flowering respectively, compared to 22.8% for the unburned plot.

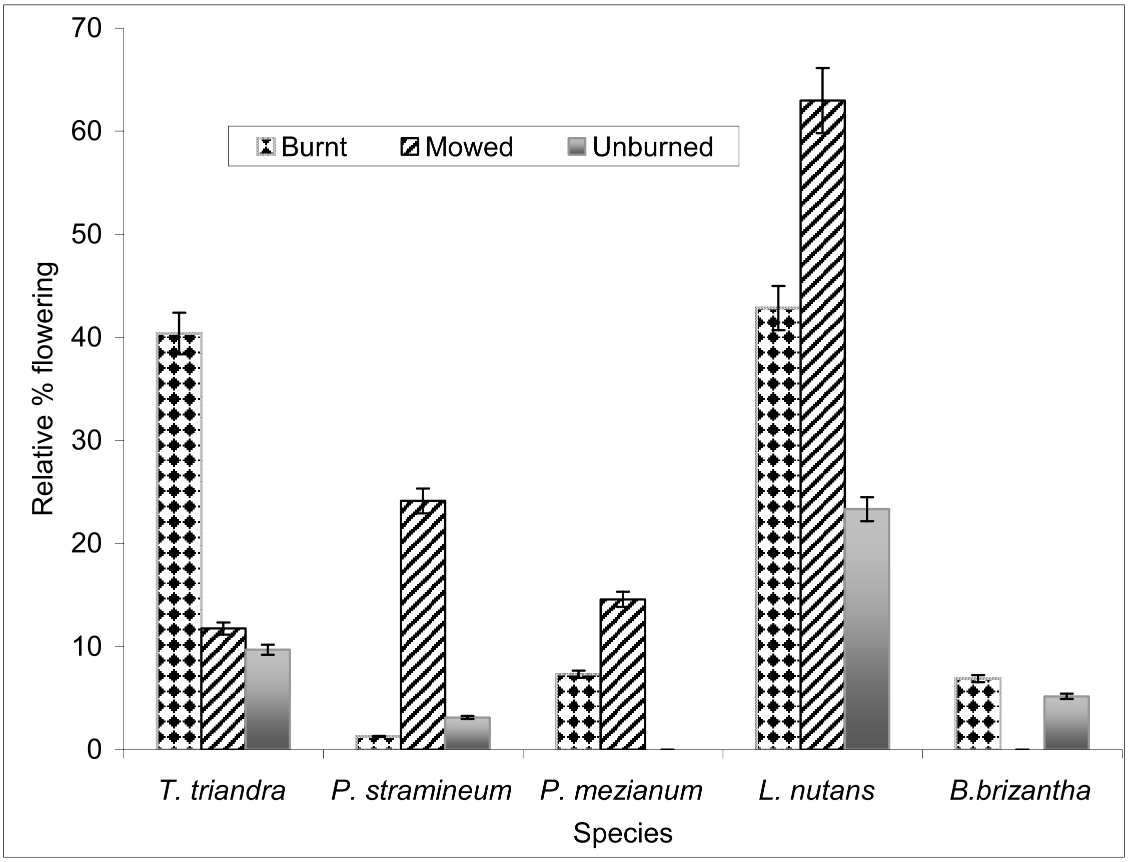

Fig. 6.2 Relative percent flowering by the major grass species in the three treatments.

## 6.5 DISCUSSION

### 6.5.1 Changes in fire temperatures

Fire temperature fluctuated both horizontally and vertically during the burn, with higher temperatures being recorded on the ground level compared to other heights. The biomass or fuel available for burning was high but the months preceding the burn were untypically wet, rains having fallen in January and February (Fig 3.2). The available biomass was suitable for a hot fire, which is good for bush clearing.

Few studies in the East African savannas have monitored vertical and horizontal fire temperature profiles, and there were hardly any with which a comparison could be made. Even fewer studies have conducted burning trials in such a big area. Tchie & Gakahu (1984) burnt a big part of Kiboko but did not report the area or the temperature profiles. Though the burn was not replicated, the fairly uniform physical and vegetation conditions of the burn area suggest that this is a typical fire in this area, and the results can be applied in areas with similar soils, slope and vegetation.

The fluctuations in the temperature profile were attributed to heterogeneity of the fuel biomass, and the changes in wind speed during the burn. Eltringham (1976) also reported that fires at the Ruwenzori National Park, Uganda, were not uniform. Boo *et al*. (1996) reported mean surface fire temperature of 489 $^{o}$C -596 $^{o}$C in a semi-arid area of Argentina with much less biomass though they used fine wet fuels.

Given the high biomass accumulation, it is suggested that ranchers in Laikipia burn their ranges at least once every five years to prevent incidences of wild fires since these rangelands receive above normal rains at least once every five years (Pratt & Gwynne 1977; McClanahan 1996). Just after the burn at Mpala, at least 15 ranches within Laikipia experienced hitherto unprecedented wild fires, mainly attributed to biomass accumulation as a result of *El Nino* induced heavy rains of 1998/1999. These wild fires consumed thousands of hectares of herbage, leaving ranch managers vulnerable to *La Nina*, the inevitable drought phenomenon that follows the *El Nino*. Such fire disasters could have been prevented if prescribed burning was used.

### 6.5.2 Effect of fire on *Acacia drepanolobium* and other woody species

Fire damage on *A. drepanolobium* trees was minimal, and even those that had a high degree of fire damage soon coppiced. Most of the trees up to 150 cm in height had a severe fire damage index, where the average temperatures were 250 $^{o}$C. Though temperatures of over 500 °C were attained at ground level, even the small sized *A. drepanolobium* were not killed. This indicates that *A. drepanolobium* is adapted to fire.

Only 16% of *A. drepanolobium* trees were top killed, a relatively low percentage compared with the findings of Oba (1990). Top-kill is a function of fire intensity and flame height as well as availability and quality of fuel at higher elevations. Given the sparse nature of *A. drepanolobium* canopy (chapter 7), fire intensity at higher elevations above the soil surface was low, as demonstrated by the vertical temperature profile (Fig. 6.1).

Burning of savannas for experimentation and management purposes has mostly resulted in the death of many *Acacia* trees and shrubs, e.g. *A. tortilis* (Oba 1990). In some cases, burning is followed by an increase in the recruitment through germination of seedlings, e.g. *Acacia tortilis* in the Turkwel valley (Oba 1990), *Acacia sieberiana* in Queen Elizabeth National Park, Uganda (Sabiiti & Wein 1988). However, the response of *A. drepanolobium* to burning was almost the opposite, with no deaths of adult trees, and a suppression of seed germination.

Coppicing of *A. drepanolobium* is further evidence that it may well be adapted to fire. It is significant that only smaller trees, which had a more severe fire effect, coppiced. Does this suggest that *A. drepanolobium* is prudent in its allocation of resources and only severely damaged plants coppice? It is tempting to argue that trees most affected by fire had the greatest number of coppicing stems, but it was not possible to quantify the extent of fire damage.

Coppicing is thus a strong indicator that *A. drepanolobium* is well adapted to fire in the savannas. Even if its crown is consumed by fire, and smaller stems are burnt out, the tree quickly produces coppice material, which grows relatively fast (chapter 7) to ensure its survival. Trees that were less affected by fire did not coppice, suggesting an efficient reallocation of resources. Coppicing (which is empirical evidence of apical dominance), is thus a strategy of the tree to adapt to environmental stresses like fire and harvesting. The number of coppice shoots that emerge suggests a form of insurance for survival.

The coppicing seen, especially in the lower height classes, attests to this. Apical dominance was expressed more strongly in the shorter trees because they had a greater percentage of top-kill compared with taller trees. Coppicing has also been reported for other *Acacia* species, especially young trees after burning e.g. *A. tortilis* (Oba 1990) and *A. sieberiana* (Sabiiti & Wein 1987; 1988). Other tree and browse species were significantly affected, for example, *L. europaeum* was eliminated, while *C. farinosa* shrubs were still dying, none showing signs of fully recovering from the burn. These other species may not be as well adapted to fire as *A. drepanolobium*, and fire may be used to them from land.

The growth in both height and diameter of *A. drepanolobium* after the fire was greater than the mean growth rate reported in chapter 4. Several reasons could have contributed to this, the most proximate being the release of nutrients tied up in the plants that were burned.

Most of the trees less than 150 cm in height coppiced after the fire. Most of the growth recorded in this height class was from coppice. The high mean number of coppicing stems suggests that the range can quickly revert to being bushy. However, it is reported in chapter 7 that the number of coppicing stems reduces to one or two with time as apical dominance sets in.

*Acacia drepanolobium* seeds that were placed below the soil surface germinated while on the surface had very little germination. It was shown in chapter 5 that *A. drepanolobium* seeds exposed to fire do not germinate. The germination from buried seeds may indicate that lethal temperatures for germination were not attained below the soil surface. Most of the surface seeds were charred beyond recognition, and recovery rate was low, about 34%, most evidently burnt. About 70% of buried seeds were recovered, the 30% loss suggests that a third agent may have removed them, probably rodents. Keesing (1998, 2000) showed that *Saccostomus mearnsi*, the commonest rodent in this ecosystem, predated on seeds of *A. drepanolobium*. Birds also predated on the seeds of *A. drepanolobium*, but the extent of this was not investigated.

These results are similar to those reported in chapter 5, which suggested that fire negatively affects the germination of *A. drepanolobium* by killing its seeds. Though fire may kill seeds of *A. drepanolobium*, a few still escape and germinate. However, the results here are conclusive that fire reduces, not enhances, the germination of *A. drepanolobium*. Fire can thus be used as a tool to control the regeneration of *A. drepanolobium* from seed.

There are many reports of *Acacia* species that have not been eliminated or seriously affected by fire, e.g. *A. brevispica* (Thomas & Pratt 1969), A. *seya*l *var seyal* (Pratt & Knight 1971), *A. senegal* and *A. gerardii* (Harrington & Ross 1974) and *A. sieberiana* (Sabiiti & Wein 1988). The overall effect of fire on *Acacia* trees would depend on the intensity and frequency of burning (Sabiiti & Wein 1987). Pellew (1983) predicted that repeated burning would eliminate the *Acacia* woodlands of Serengeti within 25 years. However, Sabiiti & Wein (1988) suggested that fire was not an important factor controlling regeneration of *Acacia species*, but Ross *et al*. (1976) stated that fire was instrumental in preventing regeneration of *Acacia* woodland in Kidepo Valley National Park, Uganda.

### 6.5.3 Effect of fire and mowing on the herb layer

Fire and mowing reduced foliage cover of the main herb layer species. The results demonstrated that fire could affect species composition and cover in this range. Fire may have stimulated the germination of the seeds of some herb layer species, possibly by providing gaps. It is also possible that these 'new species' were missed during the initial cover and compositional analysis because of the dense cover by the dominant herb layer species, and were not 'new' to the habitat. A significant result was the proliferation in flowering in the burned and mowed plots.

The relatively high flowering in the burned and mowed plots in comparison to the control plot could have resulted from a number of factors including *inter alia*, i), increase in available space or gaps created by fire defoliation (O'Connor & Everson 2000) allowed plants to express fully their physiological potential. ii) Adaptations of species to forces of defoliation like fire (Eltringham 1976), which necessitates that the plants complete their reproductive cycle quickly. iii) The plants were freed of dead or moribund material that may have stifled growth and reproduction (Edroma 1981). iv) New growing material that took advantage of the available nutrients to grow quickly and set seed (Edroma 1981). v) Growth nutrients released from burnt material and soils (Edroma 1985), which enhance growth and maturation of plants. These are all possibilities, but a question that arises is why more flowering in *Themeda triandra* after fire, and *L. nutans* after mowing?

A probable explanation is that *Themeda triandra* was quick in taking advantage of the gaps created by fire defoliation, increased light and the minerals released from the soils and burned material e.g. nitrogen and phosphorus (Edroma 1985; McNaughton & Chapin 1985), to grow and reach maturity quickly. In addition, *T. triandra* has the ability to develop tillers above the soil surface after fires (O'Connor & Everson 1998). The apical buds of *T. triandra* are usually located close to the ground surface where the bases of established plants which are resistant to fire protects them from burning (Edroma 1984), thereby giving the plant a head start in vegetative regeneration after fires. Flowering quickly may also be a strategy to ensure propagation of new plants in the midst of heavy defoliation.

Another possible reason could be that fire or the smoke triggered germination of *T. triandra* seeds (Baxter *et al.* 1994), although Ndawala-Senyimba (1972) suggested that removal of litter was enough to stimulate germination, and the emerging seedlings grow vigorously until they set seed because of the improved soil conditions.

*Lintonia nutans* may be adapted to grazing at low levels, and the removal of dead material may have left it with more resources to grow faster and set seed. Clipping has been shown to stimulate tiller production (McNaughton 1979), e.g. in *Brachiaria platynota* (Edroma 1985). Though mowing is not the same as grazing (Heady 1975), the end result is defoliation. The increase in flowering of *L. nutans* after mowing may be ascribed to the resultant vigour in growth because of new plant parts.

Stoloniferous and rhizomatous species, e.g. *P. mezianum* and *P. stramineum*, invest in a few reproductive culms, thus may not flower as profusely as species like *T. triandra* (O'Connor & Everson 1998). The difference in flowering between the species is probably due to inherent differences among the species to respond to disturbances such as mowing and fire. The increase in flowering after fire and mowing for these grass species has implications for management of these ranges. One is an indication that species composition may change towards the direction of those that are flowering vigorously.

### 6.5.4 Management implications of burning and mowing

The effect of fire on the trees and shrubs demonstrates the potential of fire in clearing shrubbery on this type of range. Though no *A. drepanolobium* trees were killed, the fact that few of its surface seeds germinated is a pointer that fire can effectively control its spread in cases where it has become a bush problem. Fire also greatly reduced many woody species within the range, eliminated some shrubs like *L. europaeum*, and significantly reduced others, e.g. *R. natalensis* and *Grewia* sp. In the past, harvesting and chemical control (Outrum 1970) were unsuccessfully tried for eliminating trees on a nearby by ranch (Ol Pejeta).

It is suggested that a once-off burning of a range with the type of fire used in this experiment may not be sufficient to adequately control brush, especially *A. drepanolobium* that seems well adapted to fire. Though shrubbery may be eliminated, repeated burning may be needed to reduce tree and shrub density. Though *A. drepanolobium* coppices after fire, it is suggested that repeated burning may exhaust the resources used in coppicing, and completely eliminate regeneration from seed, the major means by which bush encroachment takes place (Kriticos *et al*. 1999).

Mitigation of bush encroachment should be a long-term plan, and be made part of the overall ranch management. In addition, quicker results may be obtained by combining fire with other means of bush control like physical harvesting of trees and shrubs. Fire offers the best option to open the shrub layer, while harvesting, apart from clearing the range of shrubs on a short term, also offers a source of forage security during droughts and additional income from the sale of forage and fuelwood.

It is also suggested that ranches should mow and bale hay especially after heavy rainfall events. This hay can then be used during prolonged droughts, and also be sold off for additional income. Mowing may also help prevent incidences of wild fires such as occurred over Laikipia after the *El Nino* rains. Though the costs of the operation may be high, it is cheaper than the loss of hundreds of livestock (including genetic material) as happened in the last major drought 1999-2000.

Since fire is an important phenomenon in the grassland dynamics, it should be used to manage the range. Its effects should be continuously monitored to gain more knowledge and for it to be put to the best use possible, especially the best time of burning for the varied management goals of different ranches. In the same light, more investigations should be made on the effects of mowing, with the aim of fully understanding its effects and the ensuing dynamics as well as making it an efficient tool of profitable rangeland management.

# 7 CHAPTER SEVEN: CHRONO-SEQUENCE RE-GROWTH AND CHARCOAL PRODUCTION IN *ACACIA DREPANOLOBIUM*

## 7.1 INTRODUCTION

Fuel-wood is the primary source of cooking energy for the majority of the world's population (Young & Francombe 1991; Lew & Kammen 1997; Kennedy 1998). In Kenya, over 75% of the people use fuel-wood in either firewood or charcoal form, as it is the cheapest and most accessible source of energy (Bradley 1988). Most of the charcoal comes from forests in the rural areas and is later transported for use mostly in the urban areas (Chidumayo 1984). This practice has resulted in a massive depletion of woody vegetation (Young & Francombe 1991) and fuel-wood shortages are becoming critical (Baumer 1990). Barnes (1991) estimated that Kenya, which by then had an annual deforestation rate of 1.5%, stood to lose most of its indigenous forests by the year 2040. Harvesting trees and shrubs for charcoal production may eventually result in the degradation of vegetation and land resources, and the start of the desertification process (Baumer 1990). Selective extraction of woody species for either charcoal or firewood may induce fundamental changes in the composition and physiognomy of forests and woodlands, while indiscriminate extraction may lead to undesirable ecological consequences.

There is an urgent need to develop environmentally sound methods of sustainable fuel-wood production and exploitation. In Kenya, considerable effort has been expended on alleviating fuel-wood shortage through the introduction of fast growing exotic trees, agroforestry, and use of energy saving stoves (Lew & Kammen 1997; Bradley 1988). Conventional agroforestry approaches have met with little success because of inappropriate species, long cropping intervals, and inadequate husbandry techniques used by the harvesters, mostly the rural poor (Young & Francombe 1991). However, little attention has been paid to the sustained cropping and improvement of indigenous trees and shrubs for fuel-wood production.

Exploring the possibility of using indigenous trees and shrubs for sustained yield harvesting is a very attractive and potentially viable economic and ecological alternative. This is especially so in arid and semi-arid areas which have numerous and often extensive stands of tree and shrub species. Young & Francombe (1991) proposed *Tarchonanthus camphoratus* (leleshwa) as a candidate for sustained charcoal production. *Acacia* *drepanolobium* also seems to be ideally suited for sustained harvesting, because it appears to: 1) coppice readily after harvesting; 2) have a relatively fast growth rate; 3) be fire tolerant; 4) occur in mono-specific stands at relatively high densities; 5) have hard wood; 6) be of relatively low forage value to herbivores and, 7) harvesting *Acacia drepanolobium* for charcoal production can help pay for the costs of clearing and provide employment because income from charcoal is an attractive supplemental source of revenue. In order to propose a species for such use, there is need for quantitative estimates of its growth before and after harvesting, and its biomass and charcoal yield (Deshmukh 1992). Such information will be an invaluable basis for its informed management and conservation.

In the Laikipia ecosystem, many ranchers in *Acacia drepanolobium* areas believe that it has increased its density over the last 30 to 40 years. Some ranchers have labelled it a problem species because it, a) coppices readily in response to top kill by fire or harvesting, b) is of low forage value since it is heavily defended against herbivory, c) is increasing in density and, d) has not been successfully controlled by chemical and physical means. On many ranches large strips of *Acacia drepanolobium* are cleared for roads, paths, and to create grass leys, with most of the wood being used in traditional earthen kilns for charcoal production or as firewood (pers. observation).

## 7.2 OBJECTIVES OF INVESTIGATION

The aim of this study was to investigate whether *A. drepanolobium* could be used on a sustainable basis for the production of charcoal. This required knowledge of stand and tree yield, and the rate at which a stand could replace itself after harvesting. The objectives of this chapter were, therefore, to develop predictive equations for determination of yield of woody biomass and of charcoal, and to study the rate of regrowth of coppicing stands through chrono-sequence analysis.

## 7.3 MATERIALS AND METHODS

### 7.3.1 The species *Acacia drepanolobium* and study sites

*Acacia drepanolobium* is the dominant species in arid uplands with impeded drainage where it forms nearly mono-dominant stands, especially on black cotton soils (Young *et al*. 1997; Young *et al.* 1998). A detailed description of the species and the study area is included in chapter 3.

### 7.3.2 Procedure

#### *7.3.2.1 Destructive sampling*

Sixteen *Acacia drepanolobium* trees ranging in stem diameter (at the base) from 0.6 cm to 14.2 cm were harvested from natural stands. Sampling was designed to ensure a representative range of diameters. The harvested trees were sectioned into classes based on 1 cm increments of diameter. For each section, the leaves, galls, fresh growth, twigs (defined as < 2 cm diameter), and woody material (defined as > 2 cm diameter), were separated and air-dried to constant weight. These sections were weighed to the nearest gram for leaves, galls, fresh growth and twigs and to the nearest 50 g for woody biomass using electronic scales. The lengths of all the twigs and stems were measured to the nearest centimetre to estimate the total running length of twigs and stems in each tree.

#### *7.3.2.2 Charcoal Yield*

Local charcoal burners were contracted to harvest trees of *Acacia drepanolobium* and burn the wood for charcoal. Before harvesting, an overstorey vegetation inventory was undertaken in order to estimate species composition and density using 15 randomly sampled belt transects (50 m by 5 m). The heights and diameters (25 cm above ground) of all trees and shrubs falling within the transects were recorded.

Plots of 0.17 ha from which *Acacia drepanolobium* were to be harvested for charcoal were marked out. Only *Acacia drepanolobium* trees were put into the kilns. For each piece of wood used, a) length of stem, b) circumferences at the tip and at the base of the stem (these were later converted to diameters), and weight of stem to the nearest 50 g were measured using an electronic scale. Charcoal operators then arranged the wood horizontally into earthen kilns and lit them using methods that represented current practice. The charcoal produced was harvested and weighed to the nearest 50 g. Eight kilns were used in this study. The entire process from harvesting the wood to charcoal production varied from 6 to 8 weeks. Charcoal producers made all decisions concerning type of kiln, arrangement of woody stacks, pieces to go in, and time of pyrolysis.

#### *7.3.2.3 Chrono-sequence regrowth of coppicing stands*

Four stands from which *Acacia drepanolobium* had been harvested respectively in 1984, 1993, 1994, and 1995 were located and used for determining rate of regrowth. All the four stands were found in Eland Downs, a neighbouring property. For each stand, the density, species composition, and stand structure (heights and diameters) were estimated by means of three belt transects (50 m by 5 m) in November of 1996. An unharvested stand adjacent to the 1984 plot was also inventoried. The number of coppice stems per individual in each regrowing stand was recorded. These measurements were repeated in 1998.

### 7.3.3 Analysis

Dry weight and diameter measurements were transformed to natural logarithms (ln (x + 1) to standardize for zero values) and least squares linear regression analysis of the relationship between biomass of each plant component (leaves, fresh growth, thorns, galls, twigs, woody biomass, total biomass, and stem diameter was undertaken. Only the equation for woody material (> 2 cm) was used to estimate biomass available for charcoal yield because the smallest piece of wood that was used in the kilns had a diameter of 2 cm. Distribution of biomass among the plant parts was calculated on a percentage basis.

Total biomass of each regrowing stand was calculated as the sum of estimated biomass of each individual using the predictive equation derived above. Linear regression analysis for the relationship between charcoal yield per hectare and woody biomass was undertaken. Growth rates of the coppicing stands per year were calculated based on the mean increase in heights and stem diameters per site. Growth rate (height and diameter) and increase in woody biomass were calculated for each stand based on relationships derived from the destructive sampling. The regrowth data enabled estimation of time taken for a harvested stand to recover to harvestable levels.

## 7.4 RESULTS

### 7.4.1 Allometric relations of *Acacia drepanolobium*

Basal diameter was an excellent predictor for the dry weight of an *Acacia drepanolobium* tree (Fig. 7.1). The relationships between dry weights of different tree sections and their respective stem diameters were strong and positive for galls (y = 1.91 x + 2.71, $R^2$ = 0.92) and thorns (y = 1.79x + 2.55, $R^2$ = 0.91), but weak for leaves (y = 0.92x + 3.96, $R^2$ = 0.17) and fresh growth (y = 1.01x + 2.98, $R^2$ = 0.24) (Fig. 7.2).

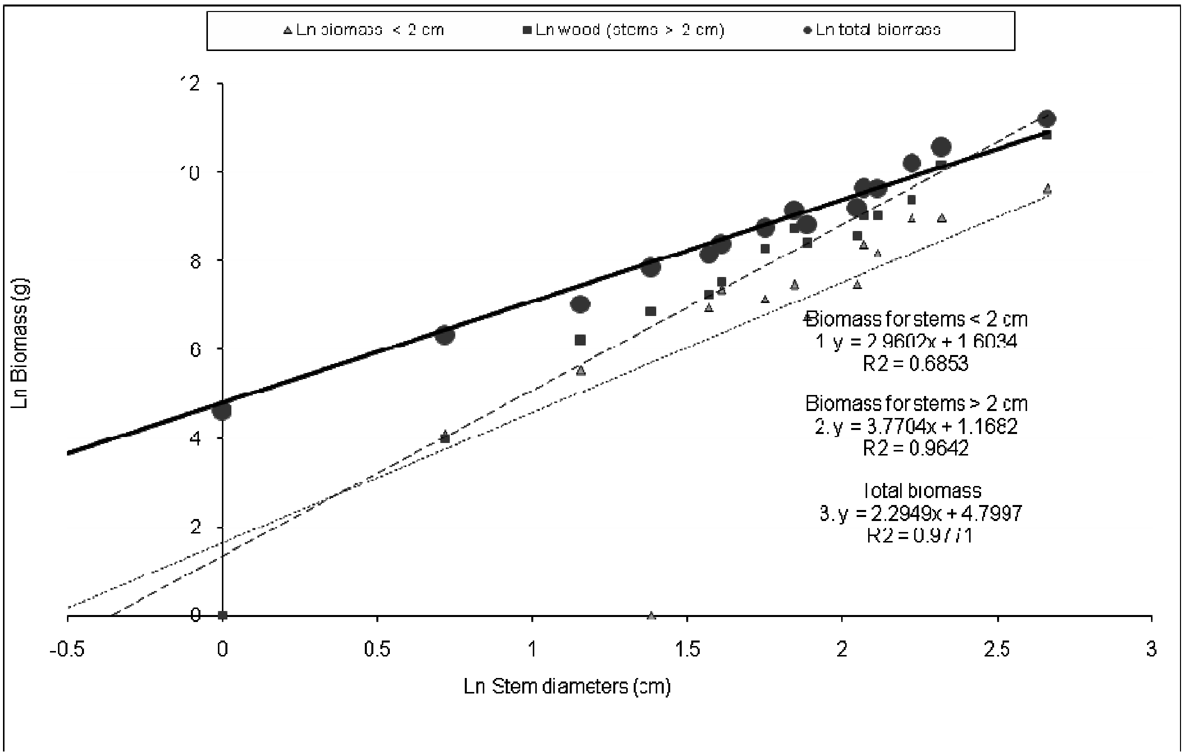

Fig. 7.1 Natural log-log relationship between biomass and stem diameter for woody plant components. Solid line with big black blots represents relationship between total biomass and diameter, the broken line with squares is woody material > 2 cm diameter, and the thin line with triangles is biomass from twigs < 2 cm. Regression equations and the $R^2$ values are inset.

Regression analysis for the harvested wood that went into the kilns showed that stem diameter by length of stem had a strong relationship with the cube root of fresh weight of the trees ($R^2$ = 0.86). Useful woody biomass varied from 43 - 69 % of the entire tree biomass.

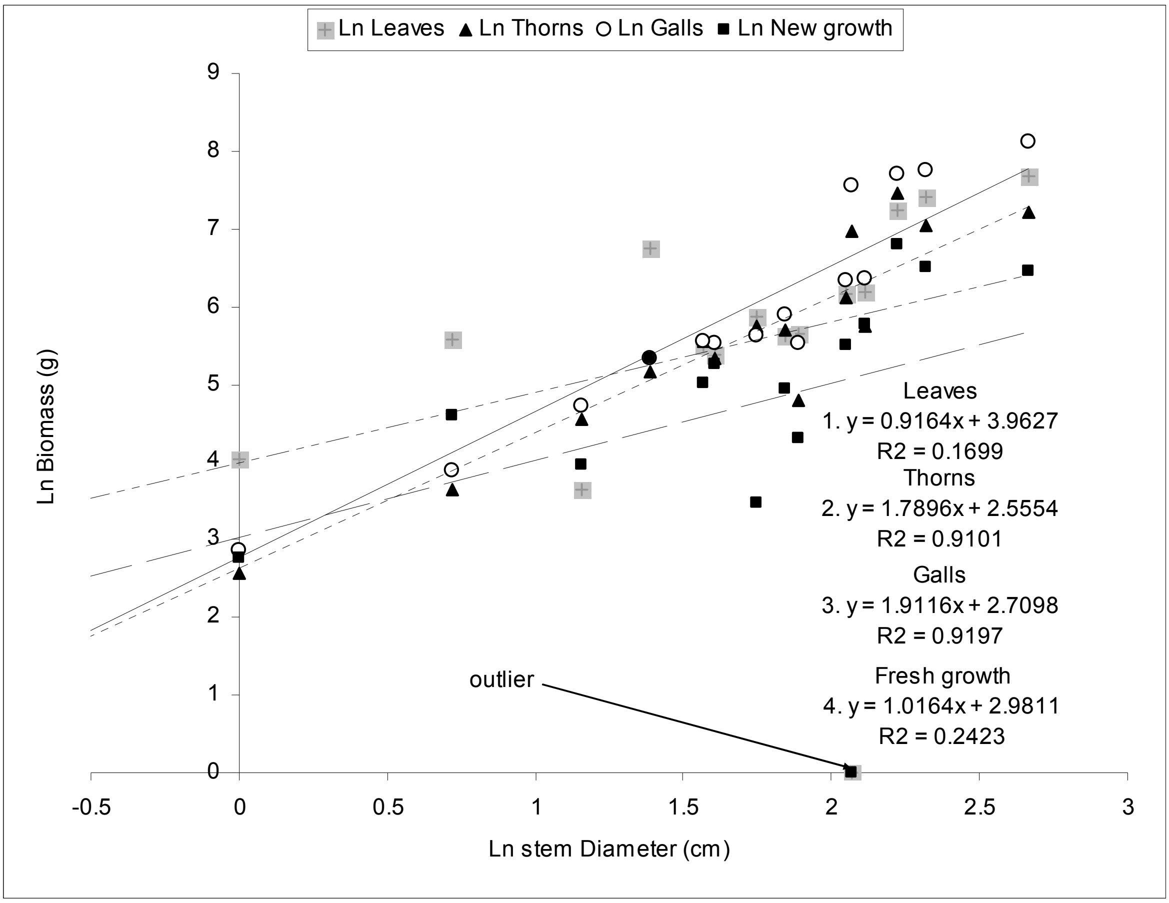

Fig. 7.2 Natural log - log relationship between biomass and stem diameter for non-woody plant components. Regression equations and $R^2$ values are inset.

### 7.4.2 Charcoal Yield of *Acacia drepanolobium*

Charcoal yield from *Acacia drepanolobium* was strongly related to the biomass of woody material (wet weight) that went into the kilns (Fig. 7.3). A total of 24.3 Mg of wood was placed in the earthen kilns yielding 3.4 Mg of charcoal at an average of 2.8 Mg $ha^{-1}$ (1.5 – 4.6 Mg $ha^{-1}$). Efficiency of conversion from wood to charcoal was low in the kilns used ranging from 10.2% to 18.2% (mean 14.2% ± 0.90 S.E.).

Linear regression equations between charcoal yield and density of *Acacia drepanolobium* from harvested plots was weak ($R^2$ = 0.31). Similarly, the relationship between biomass yield (wet weight) and density was weak, with fitted linear regression accounting for less than 20% of the observed variance.

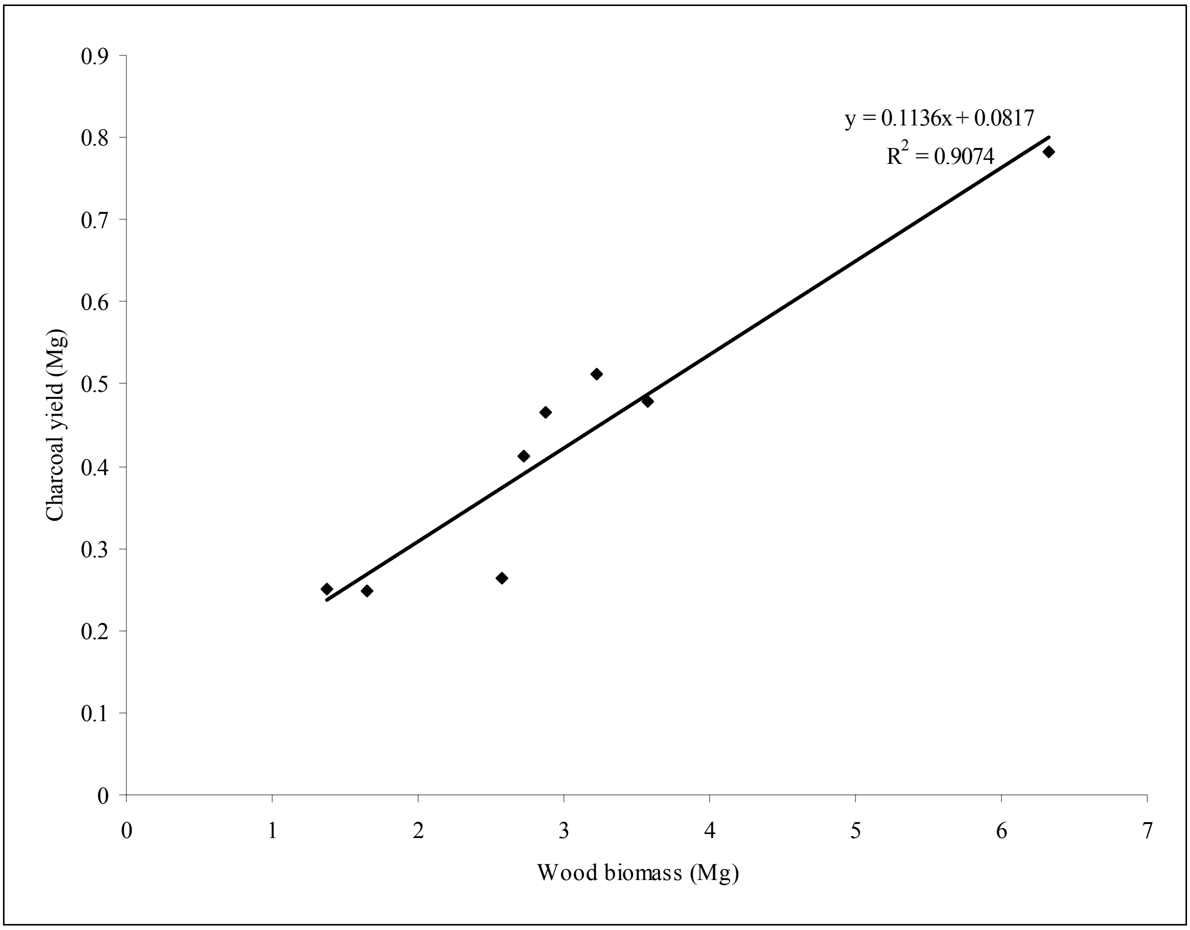

Fig. 7.3 Relationship between charcoal yield and woody biomass in kilns.

### 7.4.3 Chrono-sequence of regrowth

The density of coppicing *Acacia drepanolobium* in the four plots of different ages was 1156, 967, 933, and 933 (trees per ha) in 1, 2, 3, and 12 year old stands respectively (mean density of 997 trees per hectare). This figure is similar to density figures from nearby sites and is consistent with *Acacia drepanolobium* density for Laikipia rangelands (Young *et al.* 1998).

Coppicing trees took approximately 12 - 14 years to grow back to pre-harvest heights (Fig. 7.4). Growth in both diameter and height was almost linear. However, there were years during which growth was evidently disrupted. The three and four year old plots have similar mean diameters, suggesting that the 4-year-old plot had been stunted in growth at some time. These stands were harvested in 1994 and 1995 respectively.

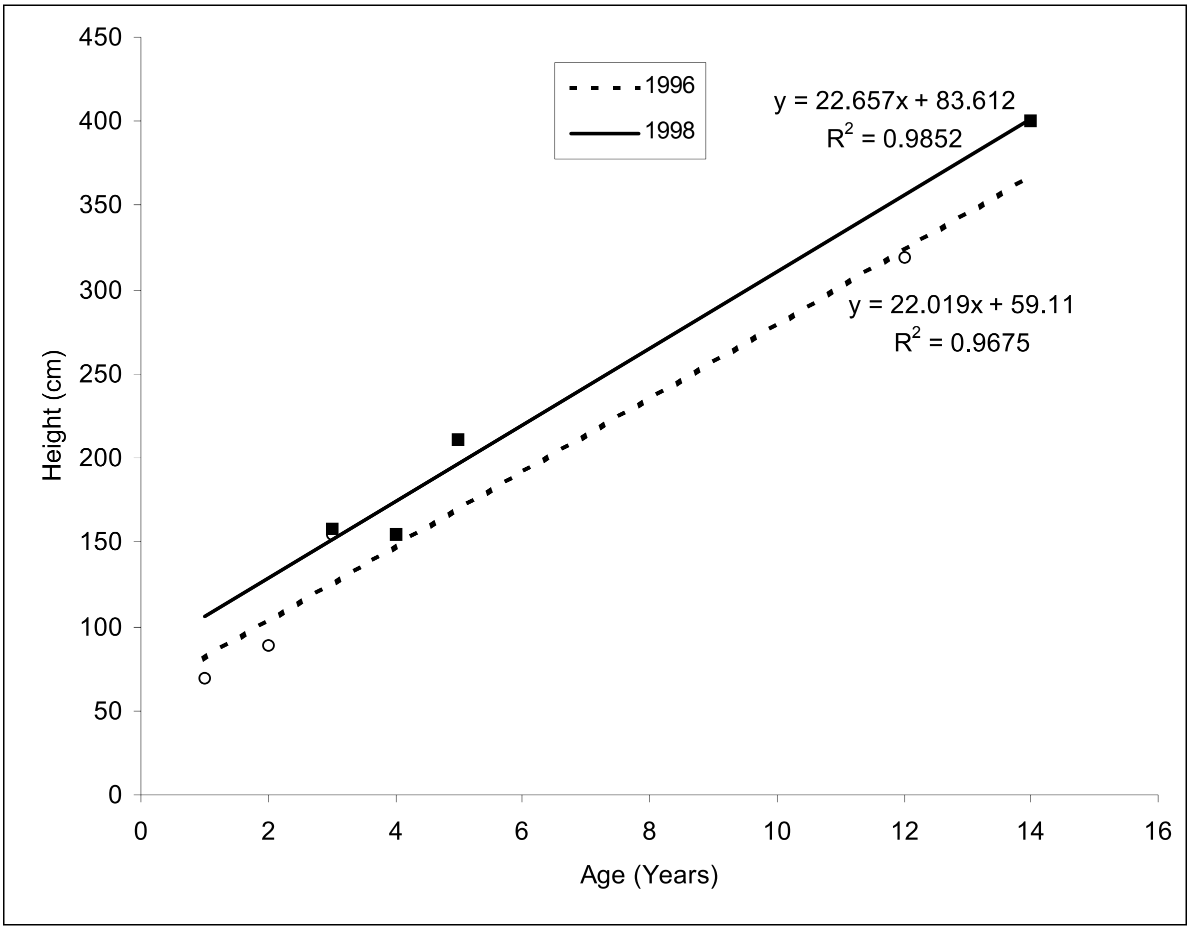

Fig. 7.4 Mean growth of coppicing stands of *A. drepanolobium* with time.

Laikipia experienced a major drought in 1994 and this could have adversely affected coppicing in the 1994 stand. Growth in height was slow for the first two years, increased in the second, and slowed in the fifth year. Similarly, the months between the two censuses were abnormally wet, and characterised by rapid growth. Increase in mean diameter within the coppicing stands mirrored that of mean heights (Fig. 7.5).

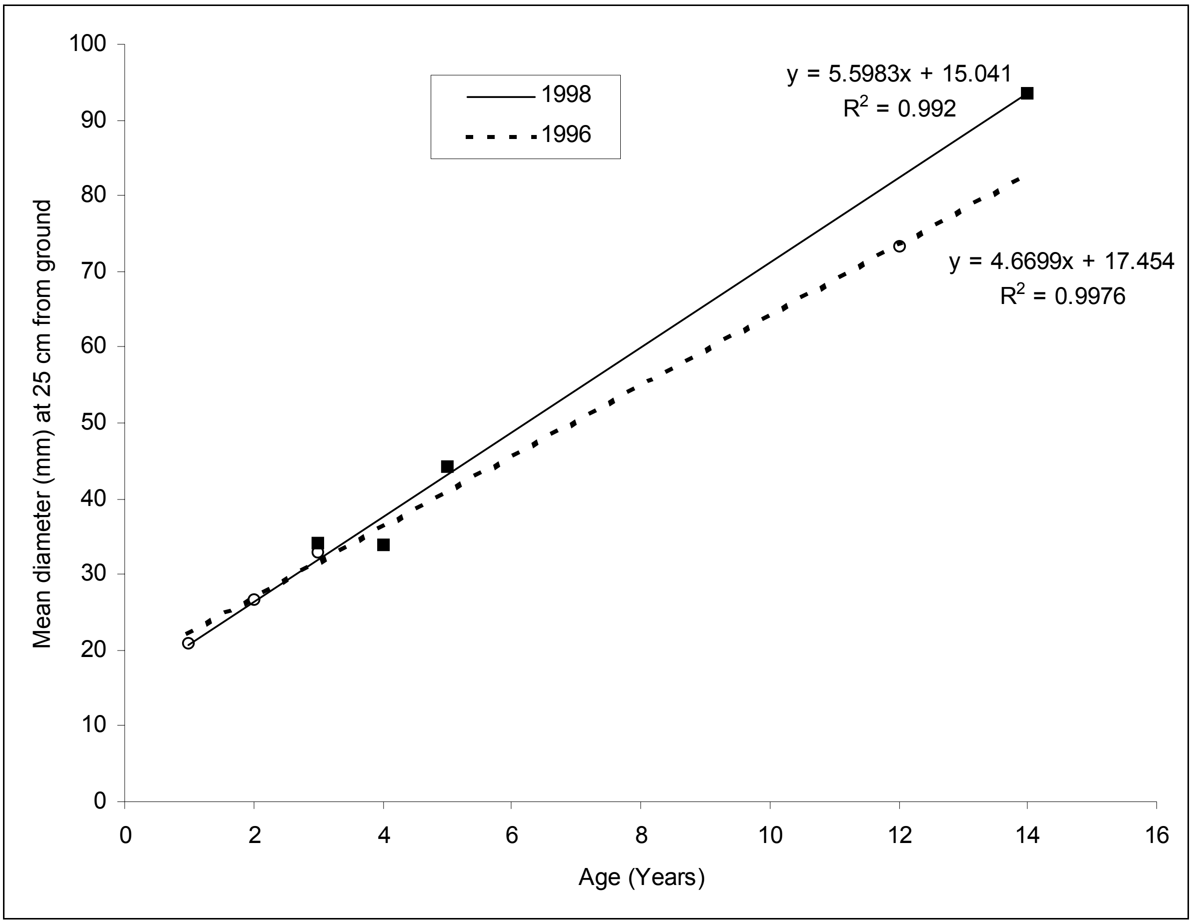

Fig. 7.5 Mean stem diameter at 25 cm from the ground, of coppicing stands of *A. drepanolobium* with time.

Stem diameter increased at an average of 2 cm in the first year. Increase in diameter is at a mean rate of 0.7 cm per year, with the maximum rate at 2.9 cm per year recorded between the 12th and 14th years. Height increased at a mean rate of 28.6 cm per year, with a maximum rate of 100 cm per year.

In the early years of regrowth, the plant also invests in a large number of coppicing stems (a max of 8 stems in the first year), which may affect its vertical growth. It took three to four years for the dominant stem(s) to emerge. Some trees continue growing to maturity with two or more stems. However, most trees have only one stem left by the fifth year. The number of stems per individual tree decreases with age from a mean of 2.8 after the first year to 1.2 after 14 years. The number of stems stabilises between the fourth and sixth years when one or two stems remain (Fig. 7.6).

Fig. 7.6 Change in the mean number of stems per tree of coppicing *A. drepanolobium* over time.

As coppicing stands age, the diameter size classes spread out for each age group with more diameter classes being represented in subsequent years (Table 7.1). The modal diameter class increases with time by about one cm per year. No seedlings were recorded in coppicing stands. The youngest plots had the largest proportion of small diameter stems while the older plots had a reduced proportion of small diameter classes and a greater representation of large stems.

Table 7.1 Mean percent distribution of diameter size classes (cm) in coppicing *A. drepanolobium*_stands of different ages in 1996 and 1998. Percent contribution of each diameter size class is indicated in brackets

| | Year of sampling and age of stand | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Diameter class | 1996 | | | 1998 | | | | | 1996 |
| | 1 | 2 | 3 | 12 | 3 | 4 | 5 | 14 | Control |
| < 1 | 1 (1.9) | | | | | | | | 12 (12.9) |
| 1-2 | 23 (44.2) | 6 (20.7) | 2 (7.1) | | | | | | 14 (15.1) |
| 2-3 | 23 (44.2) | 14 (48.3) | 10 | | 12 (40) | 12 (40) | | | 15 (16.1) |
| 3-4 | 5 (9.6) | 6 (20.7) | (35.7) | | 11 (36) | 12 (40) | 11 (36.7) | | 9 (9.7) |
| 4-5 | | 3 (10.3) | 10 | 2 (7.1) | 5 (16) | 5 (16) | 13 (43.3) | | 3 (3.2) |
| 5-6 | | | (35.7) | 3 (10.7) | 2 (6) | 1 (3) | 4 (13.3) | 1 (3.3) | 6 (6.5) |
| 6-7 | | | 5 (17.9) | 7 (25.0) | | | 2 (6.7) | | 4 (4.3) |
| 7-8 | | | 1 (3.6) | 4 (14.3) | | | | 7 (23.3) | 11 (11.8) |
| 8-9 | | | | 9 (32.1) | | | | 9 (30.0) | 5 95.4) |
| 9-10 | | | | 2 (7.1) | | | | 4 (13.3) | 1 (1.1) |
| 10-11 | | | | | | | | 4 (13.3) | 3 (3.2) |
| 11-12 | | | | | | | | 3 (10.0) | 2 (2.2) |
| 12-13 | | | | 1 (3.9) | | | | | 1 (1.1) |
| 13-14 | | | | | | | | 2 (6.7) | 3 (3.2) |
| 14-15 | | | | | | | | | 2 (2.2) |
| 15-16 | | | | | | | | | 1 (1.1) |
| 18-19 | | | | | | | | | 1(1.1) |

Table 7.2 Estimated dry woody biomass yield (Mg $ha^{-1}$) of coppicing *Acacia drepanolobium* stands at different ages distributed by diameter size class in 1996 and 1998

| | Year of sampling and age of stand | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Diameter class | 1996 | | | | 1998 | | | | 1996 |
| | 1 | 2 | 3 | 12 | 3 | 4 | 5 | 14 | Control |
| 2-3 | 0.05 | 0.05 | 0.05 | | 0.03 | 0.06 | | | 0.02 |
| 3-4 | 0.04 | 0.06 | 0.11 | | 0.09 | 0.14 | 0.14 | | 0.05 |
| 4-5 | | 0.08 | 0.16 | 0.06 | 0.10 | 0.16 | 0.42 | | 0.03 |
| 5-6 | | | 0.05 | 0.18 | 0.07 | 0.05 | 0.26 | 0.09 | 0.18 |
| 6-7 | | | | 0.86 | | | 0.26 | | 0.23 |
| 7-8 | | | | 0.80 | | | | 1.57 | 1.06 |
| 8-9 | | | | 2.63 | | | | 3.22 | 0.73 |
| 9-10 | | | | 1.13 | | | | 2.04 | 0.25 |
| 10-11 | | | | | | | | 3.14 | 1.02 |
| 11-12 | | | | | | | | 3.08 | 0.89 |
| 12-13 | | | | 1.65 | | | | | 0.64 |
| 13-14 | | | | | | | | | 2.68 |
| 14-15 | | | | | | | | | 2.15 |
| 15-16 | | | | | | | | 5.83 | 1.32 |
| 18-19 | | | | | | | | | 2.86 |
| Total | 0.09 | 0.19 | 0.27 | 7.31 | 0.29 | 0.41 | 1.08 | 18.97 | 14.11 |
| Mg/month | 0.007 | 0.008 | 0.008 | 0.051 | 0.008 | 0.009 | 0.018 | 0.113 | |

Biomass estimates showed that coppicing stands had at least 18.97 Mg ha$^{-1}$ of dry wood (Table 7.2) at 14 years or 23.71 Mg ha$^{-1}$ with a mean weight loss of 10 % during drying. The largest diameter class recorded (15-16cm) in the 14-year plot contributed one third of the total woody biomass within the plot. This estimate for 14 years of re-growth therefore falls within the range of 15.05 – 142.21 Mg wet weight ha$^{-1}$ of wood used in kilns. The estimated woody biomass data illustrates that it increases at an increasing rate with an increase in diameter.

As expected, there was a greater increase in woody biomass per unit of increase in diameter for larger (older) trees than for smaller (younger) ones. Increase of dry woody biomass averaged 0.007 to 0.051 Mg month$^{-1}$ for the first 12 years then increased to 0.113 Mg month$^{-1}$ by the 14th year. The rate of woody biomass accumulation was lower in the smaller sized diameters and increased rapidly as more trees reached ‘maturity’. This is because a millimetre increase in the diameter of a large tree will result in an increase of woody biomass far greater than a millimetre increase in a small tree since the woody biomass is a function of the tree diameter and its height.

## 7.5 DISCUSSION

Allometric measurement is a common technique for non-destructive estimation of plant biomass. Fitted linear regression equations after log transformations were excellent predictors of biomass from stem diameters. Many savanna species have been reported to have strong relationships between their weights and stem diameters: *Acacia tortilis* (Lusigi 1983), *Acacia senegal* (Lamprey 1983), *T. camphoratus* (Young & Francombe 1991), and *A. etbaica* (Okello 1996). Buech & Riggs (1989) concluded that site and species-specific models improved goodness of fit significantly although general models for all trees works well in most cases. The general models of predicting biomass from diameter worked well for this species.

Trees with diameters greater than 4 cm can contribute 43 - 69% of the biomass used for charcoal production. The remainder is used as fuel for kilns, kiln spacers, and firewood (< 2 cm diameter). Most twigs and leaves not used for charcoal production are used in covering denuded areas to encourage revegetation.

Variation in biomass that went into the kilns can be attributed to differences in tree density and population structure. Where trees were large, biomass accumulated could be greater than in plots with smaller trees, other factors being constant. The results suggest that greater wood yield was obtained from stands with a lesser density of larger trees than from stands with a greater density of smaller trees. Regression equations suggest that even in instances where the density is high and the population has relatively smaller trees compared to plots where trees are few but large, the overall woody biomass yield would be greater for the latter. Woody biomass was not in any way related to tree density or to maximum and minimum stem diameters within a stand. It can therefore be expected that an improved woody yield can be expected from a larger tree if it is left to regrow after first harvesting.

In many African countries, charcoal is produced in earthen or brick kilns, enclosures in which wood is burnt with a limited air supply. About half the wood is burnt completely to ash and the heat given off during this combustion is sufficient to carbonize the remaining wood and thereby form charcoal. This method of charcoal production obviously causes a great deal of pollution and is extremely wasteful, with almost acrid smoke billowing off, and lots of other gases and tar wasted. The tar and gasses released contain about half the total available energy of the wood in its uncarbonized form (Cunningham 1996).

Charcoal yield from the present study was low but similar to yields from earthen kilns in many studies (Lew & Kammen 1997). Efficiency was low (maximum 18.2%) and varied between kilns, which, though similar in design, are usually different because the size and composition of wood used, and because the time taken for carbonization is different. More technologically advanced kilns such as the Mark IV, Cusab Kiln, and Gayland Batch charcoal retort give efficiency rates of 25% to 32% (Cunningham 1996; Lew & Kammen 1997). These kilns could significantly improve charcoal production in rural areas. However, such kilns are usually out of the financial reach of most charcoal burners.

Coppicing in *Acacia drepanolobium* begins shortly after the trees have been cut, usually within three months, especially if rains fall shortly after harvest. The phenomenon of a reduction of number of stems with increasing age has been reported elsewhere (Young 1984). It has been postulated that large shoots continuously and increasingly suppress the success of younger shoots (Young 1984; Kennedy 1998). In *Acacia drepanolobium*, the stems appear to regenerate at almost the same time, and the reasons why some die off is not yet understood, but apical dominance would suggest that slight differences in size are soon magnified.

The mean annual rate of increase in height of 28 cm for the coppicing stands is higher than for non-coppicing stands (25 cm, see chapter 4) though the sampling designs do not allow for statistical comparisons. This is a reasonable rate for a high-density wood tree in a rainfall regime of 550 mm per annum. Maximum annual growth in height recorded was 100cm, and this followed the heavy *El Nino* rains of December 1997 - January 1998. Young & Francombe (1991) predicted that *T. camphoratus* would take about seven years to grow back to maturity. However, they did not indicate the mean heights of mature stands they sampled. Kennedy (1998) suggested that coppicing woody species have a higher growth rate than seedlings. Coppicing stems grow vertically due to strong apical dominance (Cannel 1983). Trees that coppice still protect the soil since the root stock remains in place, and for nitrogen fixing trees, fertility is maintained since root nodules are still intact. Population structure in coppicing stands is more or less even as there seems to be no recruitment of seedlings (Table 7.1). As stands mature, larger diameter size classes are increasingly represented and smaller ones phased out.

The rate of diameter increase in coppicing stands is slow initially but increases with time. Rate of increase in stem diameter by regrowing trees is important in determining the time it takes a stand to be ready for re-harvesting. Larger stems have more biomass and at a certain stage seem to assimilate biomass at a faster rate than smaller ones possibly because of a larger amount of photosynthetic material and a larger root system.

The total harvestable dry woody biomass was 20 tonnes ha$^{-1}$ for a 14 year old stand, higher than 8 tonnes ha$^{-1}$ reported for *Colospopermum mopane* (Cunningham 1996), although the rain averaged 380 mm per annum in the latter study. This gave a minimum of 3 tonnes of charcoal ha$^{-1}$, assuming 15% conversion efficiency. This is considered to be an under-estimate of the potential charcoal yield from coppicing stands. Given the regrowth rates of *Acacia drepanolobium*, a minimum of 12-14 year harvest cycle is suggested. Being a relatively small tree, *Acacia drepanolobium* is ideal for sustained charcoal production since no expensive machinery is needed for harvesting as machetes and axes suffice, and it does not have any special handling needs.

For sustainable charcoal yield from whistling thorn trees to be a reality, charcoal burners must turn to kilns that are more efficient and commercialise the production process. Increased efficiency would lead to higher yields, and probably lengthen the period before a stand is re-harvested.

# 8 CHAPTER EIGHT: RESPONSE PATTERNS OF *ACACIA DREPANOLOBIUM* TO THE PRESENCE OF *ACACIA* ANTS

## 8.1 INTRODUCTION

Highly specialised symbiotic associations have evolved independently in many different families of plants and ants (Davidson & McKey 1993 a&b). Each ant-plant host produces dwelling sites (dormatia) and supplies food to support a single resident ant colony, and many plants receive protection from herbivores, diseases and competitors in return (Hocking 1970).

Although ant-plant symbioses have become a textbook example of co-evolved mutualism, multiple-species of plant-ants are commonly found in association with a single host plant species (Janzen 1966). Previous studies (Janzen 1969; 1972) have shown that some of these resident species may be 'parasites' on the mutualistic interaction, in that they do not defend, or may actually harm the host plant they occupy. *Acacia*-ant activities may have important consequences for the population dynamics of the host trees they occupy. Their activities may affect growth rates, flowering and seed production and the degree to which herbivory can take place.

*Acacia drepanolobium* (chapter 3) produces hollow swollen thorns, which can be occupied by one of at least four ant species (Young *et al*. 1997; Stapley 1998; Palmer *et al.* 2000). It has been suggested that *A. drepanolobium* may have mutually co-evolved with these ants, with the tree providing a 'home' while the ants provide protection (Madden & Young 1992; Young *et al*. 1997). However, it is acknowledged that in many mutual relationships involving defence, the interests of the host plant and its defender may be in conflict (Wilmer & Stone 1997).

Although sharp spines (chapter 3) provide *A. drepanolobium* with a formidable defence against herbivores, belligerent ants are believed to increase its defence (Stapley 1998). The resident ants or founder queens chew entry holes into the swollen thorn bases, and use these sites to harbour eggs, larvae and workers. When the host tree's branches are disturbed, the workers of an established colony emerge from the swollen thorns and attack the invaders/intruders. In most cases, some ants would be patrolling the twigs, especially new shoots.

The resident ants commonly encountered, and which are believed to be obligately dependent on the tree, are *Crematogaster sjostedti* Mayr, *Crematogaster mimosae*

Santschi, *Crematogaster nigriceps* Emery, and *Tetraponera penzigi* Mayr (Young *et al.* 1997). The authors also found *Camponatus braunsi* Mayr and *Camponotus rufoglaucus* Jerden (*sensu lato*) together with *Crematogaster (Orthocrema)* sp. on these trees. The four ants have strikingly different effects on herbivory, production of extra-floral nectaries, host tree canopy architecture, tree growth and reproduction, and the community of insects and other organisms associated with the host tree (Young *et al*. 1997).

Resident ants provide host trees with varying levels of protection against browsing damage. The ecological fates of individual trees are intimately linked to the species of ants occupying them. The acacia ants seem to be distributed on the host plant according to height of the tree. However, this has not been investigated beyond doubt. ‘Battles’ between different species for the control of the tree (resource) have been observed several times. These two facts have led to speculations on why the four ant species occur on a seemingly fine and uniform resource. A succession theory has been suggested (Young *et al*. 1997; Stanton *et al.* 1999; Palmer *et al*. 2000) but there is not enough quantitative data to support such a theory.

A competition-colonisation trade-off may lead to succession dynamics in resident ant species over a tree’s lifetime. Trade-offs between competitive ability and colonisation ability may at least be partly responsible for the continued co-existence of these four mutually exclusive ant species, which compete intensely for the *A. drepanolobium* host plant. If such trade-offs do exist, it can be predicted that individual *A. drepanolobium* trees, as they age, will experience successional changes in their species of resident ants. However, the consequences of these trade-offs on the population dynamics of *A. drepanolobium* are unknown.

*Acacia drepanolobium* produces most of its nectar in leaf glands on vulnerable new growth, and the nectar produced varies with resident ant species (Young *et al*. 1997, Palmer *et al.* 2000). Very little nectar has been found on *A. drepanolobium* or *A. zanzibarica*, another E. African *Acacia* species that produces swollen thorns in which ants live (Wilmer & Stone 1997). During seasonal rains, large numbers of worker ants feed from, and actively defend, nectar producing leaf glands near the tips of growing shoots. The thorns on these shoots take at least a week to harden, and so the nutritious forage cannot be defended mechanically.

## 8.2 OBJECTIVE OF INVESTIGATIONS

The foregoing introduction raises several questions;

(i) How do the four mutually exclusive species survive on a seemingly fine and homogeneous resource base?

(ii) Do these four ant species have any effect on the population dynamics of *A. drepanolobium* and, if so, how and at which stages? Are the responses of *A. drepanolobium* to the different ant species similar or different?

(iii) If *A. drepanolobium* is formidably defended by both ants and spines, to what extent do they limit herbivory?

(iv) To what extent do the four ant species replace each other, and what are the likely consequences of these changes to the population dynamics of *A. drepanolobium*?

With the goal of determining how acacia ants affect the population dynamics of *A. drepanolobium*, this study specifically quantified ant distribution in an *A. drepanolobium* ecosystem, documented ant turn-overs, and monitored the response of the host trees to the presence of the different ants, particularly in relation to growth, changes in canopy volume and structure, herbivory by mammals, flowering, seed production, and tree mortality.

## 8.3 METHODS

The study area and site was described in chapter 3. See also annex 1 for more details.

### 8.3.1 Distribution of ant species on *Acacia drepanolobium*

Ant species occupying *A. drepanolobium* trees were monitored on 1800 tagged trees in six herbivore treatments (chapter 4). Tree height, diameter at 25 cm from the ground, resident ant species, and tree mortality were recorded in March 1996, September 1996, January 1997, September 1997, and February 1998.

### 8.3.2 Effect of ant species on aspects of *Acacia drepanolobium* demography

On a sub-sample of 540 trees (chapter 4, section 4.2.4), the resident ant species, tree height, diameter at 25 cm from the ground, canopy volume, growth of tagged twigs, flowering, and herbivory of twigs by mammals, were monitored in March 1996, June 1996, January 1997, May 1997, September 1997, February 1998, May 1998 and September

1998. In addition, two sites in which *A. drepanolobium* was flowering (chapter 5) were used to monitor flowering and seed production of trees occupied by different ant species.

### 8.3.3 Ant species ‘take-overs’ in *Acacia drepanolobium*

By monitoring ant species inhabiting tagged trees, ant turnover was also monitored. In addition, an 'artificial ant war' was staged among different ant species by tying together branches from two trees, which had different ant species. In this 'artificial war' each of the four ant species was 'forced' to fight with each other and each pair of 'fights' was replicated six times. Tree heights with different ant species were measured and their branches tied together. The ant movements on the branches were monitored but the ant mortality was not recorded. Three trees were used in each 'fight' and the results recorded at the end of the day. Four days later, the situation was evaluated again.

### 8.3.4 Gall diameters on trees occupied by different ant species.

For each of the four ant species, ten trees were randomly selected and their heights measured. A twig on each tree was randomly selected and the diameter of the most distal gall measured to the nearest 0.1 cm using a dial calliper. The diameter of the second gall from the tip was also measured. In addition, the distance between the twig tip and the position of each of the two galls were also measured to the nearest 0.1 cm.

### 8.3.5 Data Analysis

A Chi-square test was done to determine if the ant species differed in the proportion of trees occupied, against an expected frequency of equal amounts irrespective of the herbivore treatments.

Conditional probabilities of ant species take over were calculated and tabulated using data from the 1800 KLEE trees. In addition, the 'artificial war' results were expressed on a percentage basis.

The effect of the interaction between herbivore treatment and ant species on growth, herbivory and mortality of *A. drepanolobium* was analysed by split-plot analysis with herbivore treatment as the main plot effect. In addition, a repeated measures analysis with the ant species on a tree as a random effect was also done to determine the effect of ants on twig growth, number of new growing points, twig density, spine density, spine lengths, gall density, and canopy volume of *A. drepanolobium.* These analyses were used because the ants were not assigned to any trees, but chose them themselves, while trees were randomly picked. In the initial random selection of trees, little attention was paid to the resident ant species. Cattle and total exclusion treatments were excluded in the analysis of herbivory data because little, if any, herbivory took place in these treatments, and even then only on very small sized trees (chapter 4).

Spine lengths at both the distal end and those most proximal to the second gall were log transformed (base 10) and separately analysed with one-way ANOVA. The gall diameters of the different ant species was analysed by one-way ANOVA, and the means compared using Tukey-Krammer's HSD test.

The effect of ant species on flowering was analysed by log likelihood chi-square ratio using JMP IN (Sall & Lehmi 1999).

## 8.4 RESULTS

### 8.4.1 Distribution of *Acacia* ants within *Acacia drepanolobium* community

Four acacia ant species, *C. mimosae*, *C. sjoestedti*, *C. nigriceps* and *T. penzigi*, were ubiquitous within *A. drepanolobium* trees. In almost all cases, these species were mutually exclusive, each ant species colonising a single tree. Less than 10 trees out of almost 3000 surveyed during the study had more than one ant species on the same tree and no tree had more than two ant species.

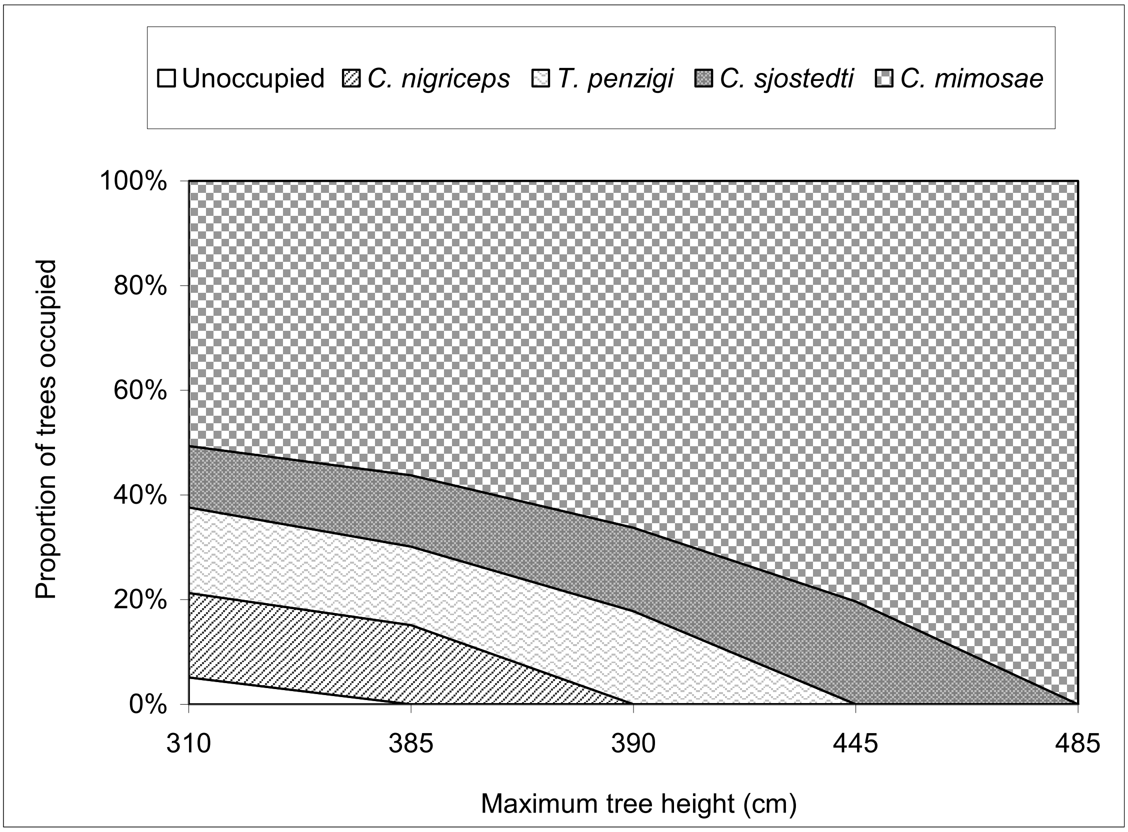

Fig. 8.1 Distribution and abundance in the ant species of *A. drepanolobium* over maximum tree heights.

*Crematogaster mimosae* was the most abundant ant species, colonising at least 50% of all trees within this ecosystem (Fig 8.1, Fig. 8.2). At any given time, some trees (less than 5%) would be unoccupied by any ant. The ant species differed in the proportion of trees occupied ($X^2$=2386.4, P<0.000, df=4).

The four ant species were distributed on the trees in a vertical spread (Fig. 8.1). *Tetraponera penzigi* was abundant in smaller (shorter) trees, but present in decreasing abundance in taller and larger (probably older) trees. *Crematogaster mimosae* and *C. sjostedti* were abundant in taller trees, though they were also present in short (younger trees), while *Crematogaster nigriceps* were abundant in trees of medium height. If tree heights are considered to approximate the age of the trees, then the distribution seems to be based loosely on tree maturity or age.

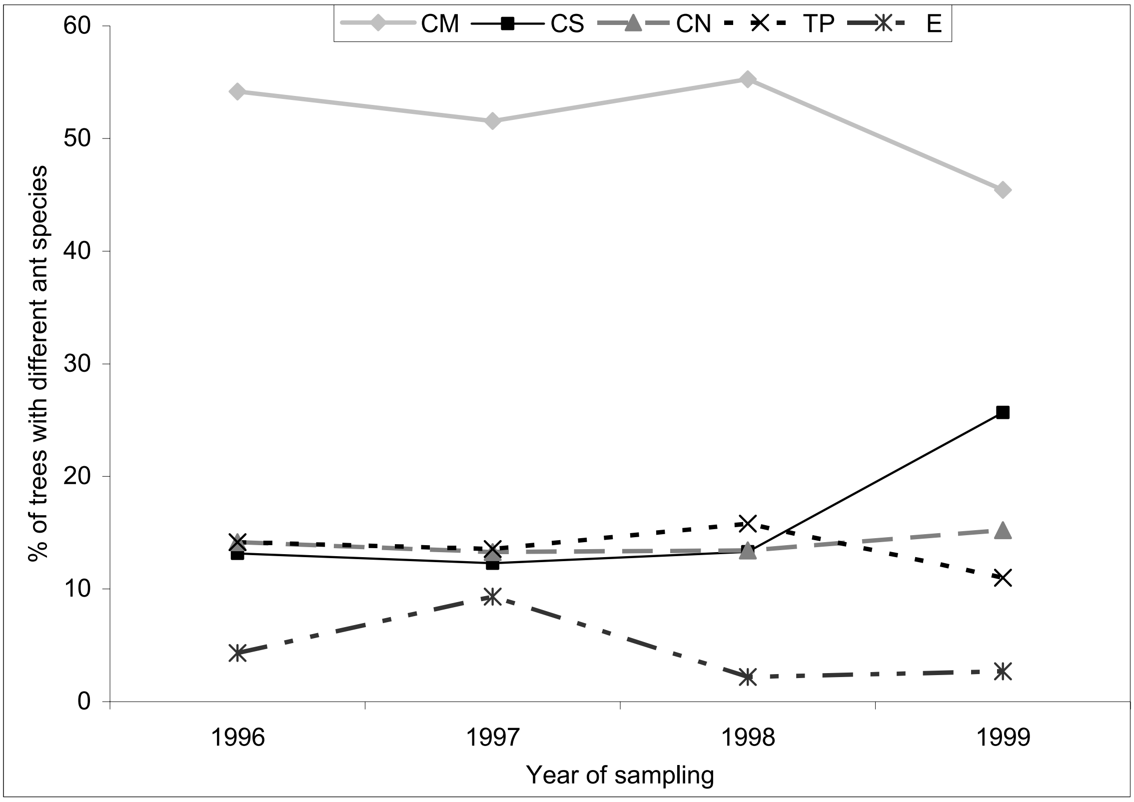

Fig. 8.2 Proportion of ant species on *A. drepanolobium* over time. Survey based on an initial sample size of 540 trees in March 1996, which had been reduced to 513 by September 1998.

The number of ants present in any gall was not determined, but the ants were numerous. Bigger trees had more galls and therefore could house more ants at any given time (Fig 7. 2, chapter 7). The four ant species had different behavioural traits. They colonised the trees on which they were found in various ways.

At least three other species believed to be *Crematogaster (Orthocrema)* sp, *Camponatus braunsi* and *Camponotus rufoglaucus* (Young *et al*. 1997), and which may be generalists, were also found on some trees, but their abundance was variable. These three ant species were present on trees that had one of the other four common ant species, especially on trees occupied by *C. sjostedti*. These three species did not live within the galls although some entered them.

### 8.4.2 Ant take-overs

Ant take-overs were observed during the course of sampling, where a species invades and takes over a tree from another species. An ‘artificial ant war’ (in which branches of two trees each with a different ant species were tied together) did not seem to mirror what happens in the real life situation. Two forms of take overs were seen. (i) when at least two branches or twigs from trees each occupied by different ant species interlocked and created a bridge between the two trees, ants from one species would use the bridge to move on to and attack ants from the next tree, resulting in the superior species taking over the entire tree. In some cases, a tenuous and often an uneasy truce was maintained on one of the trees if one species was unable to completely dislodge the other from the tree. (ii) another form of take over occurred when ants from a different species invaded a tree with a different ant species and completely dislodged the resident ants.

When colonies of two species meet, a vicious ‘war’ ensues, with opposing ant species engaging each other and falling off the tree branches in combat. These wars last between several minutes to several days. There was no conclusive evidence on which species was the most powerful, superior or competitive.

In a simulated ant ‘war’ experiment conducted in February 1998, an unusually wet period, in which trees with the four ant species were pitted against each other, take-over results were mixed after six days of observations (Table 8.1).

Table 8.1 Results of a staged 'ant war' between all combinations of ant species pairs. Each pair was replicated six times. Fights that ended in a 'draw' are not shown

|  | Winner |  |  |  |
|---|---|---|---|---|
| Loser | *C. mimosae* | *C. sjostedti* | *C. nigriceps* | *T. penzigi* |
| *C. mimosae* | - | 4 | 2 | 0 |
| *C. sjostedti* | 2 | - | 0 | 0 |
| *C. nigriceps* | 4 | 6 | - | 2 |
| *T. penzigi* | 0 | 0 | 0 | - |

*Crematogaster sjostedti* took over all *C. nigriceps* trees, and about 60% *of C. mimosae* trees, indicating that it was a superior and dominant species. *Tetraponera penzigi* defended its tree successfully against all the other ants, but in one instance had to share a tree with *C. nigriceps*. It is significant *that T. penzigi* took over a third of *C. nigriceps* trees. Both *C. mimosae* and *C. nigriceps* were the first to reach and cross the ‘bridge’ or 'war' platform, immediately engaging in combat. *Crematogaster sjostedti* reacted only when the aggressors (*C. mimosae* and *C. nigriceps*) had crossed the bridge and invaded some of the galls.

In 60% of the cases, no take-overs were recorded, with 80% of these seeing little or no combat. These results indicate that the ants were probably not ready to expand their territories, and probably the fact that take-overs and ant wars are deliberate, probably 'planned' by the ants, for expansion or foraging purposes.

On the other hand, natural wars for a take-over of a tree between two ant species almost always ended in less than 30 minutes, with a victor. In most cases the invading species (especially during and immediately after the dry season) 'surprised' the resident species and overwhelmed them. All natural wars always ended with the invaders taking control, except on two occasions, one in which *C. mimosae* was unable to take over a *C. sjostedti* tree, and another in which *T. penzigi* beat off an invasion attempt by *C. nigriceps.* Surveys on these trees showed that ant take-overs went both ways, any ant species can replace another, and these were common on trees of less 300 cm in height. The most common take-overs were those of *C. mimosae* displacing *C. sjostedti* (Table 8.2).

*Crematogaster mimosae* took over at least 11% of all the other species' host trees. It experienced the greatest loss, 17% of its trees to *C. sjostedti* in '98-'99 period. Over this period, between 75% and 83% of the unoccupied trees were colonised. The most active colonisers of unoccupied trees were *T. penzigi* and *C. mimosae* (Table 8.2).

Most take-overs occurred in the lower height classes, e.g. there were a total of 153 take-overs in trees less than 100 cm tall compared to only 72 in trees 100-200 cm tall, the relative availability of these trees (based on the time at which the data was last collected), was 20% and 30% respectively. As trees grew taller with time (See chapter 4, section 4.3.3), *C. sjostedti* and *C. mimosae* took over an increasingly greater number of trees than did *T. penzigi* and *C. nigriceps*.

Table 8.2 Conditional transition probabilities of ant species take over in *Acacia drepanolobium* from 1996 to 1999. Probabilities are in parentheses, transitions are from row to column. N is sample used

| Period | N | Species | *T. penzigi* | *C. mimosae* | *C. sjostedti* | *C. nigriceps* | Empty |
|---|---|---|---|---|---|---|---|
| 96-97 | 255 | T. P | 165 (0.65) | 37 (0.15) | 23 (0.09) | 8 (0.03) | 22 (0.09) |
| 97-98 | 205 | | 158 (0.77) | 23 (0.11) | 11 (0.05) | 8 (0.04) | 33 (0.01) |
| 98-99 | 224 | | 113 (0.50) | 26 (0.12) | 69 (0.31) | 12 (0.05) | 4 (0.02) |
| 96-97 | 975 | C. M | 44 (0.05) | 759 (0.78) | 46 (0.05) | 28 (0.03) | 98 (0.10) |
| 97-98 | 837 | | 40 (0.05) | 708 (0.85) | 54 (0.06) | 25 (0.03) | 10 (0.01) |
| 98-99 | 785 | | 20 (0.03) | 579 (0.74) | 132 (0.17) | 40 (0.05) | 20 (0.02) |
| 96-97 | 237 | C. S | 15 (0.06) | 55 (0.23) | 132 (0.56) | 16 (0.07) | 19 (0.08) |
| 97-98 | 202 | | 18 (0.09) | 58 (0.29) | 118 (0.58) | 3 (0.01) | 5 (0.02) |
| 98-99 | 189 | | 9 (0.05) | 26 (0.14) | 142 (0.75) | 10 (0.05) | 2 (0.01) |
| 96-97 | 255 | C.N | 4 (0.02) | 46 (0.18) | 10 (0.04) | 176 (0.70) | 4 (0.06) |
| 97-98 | 218 | | 13 (0.06) | 30 (0.14) | 12 (0.06) | 161 (0.74) | 13 (0.01) |
| 98-99 | 191 | | 7 (0.04) | 21 (0.11) | 13 (0.07) | 148 (0.77) | 7 (0.01) |
| 96-97 | 78 | E | 16 (0.21) | 31 (0.40) | 10 (0.13) | 8 (0.10) | 13 (0.17) |
| 97-98 | 51 | | 10 (0.20) | 16 (0.31) | 6 (0.12) | 6 (0.12) | 13 (0.25) |
| 98-99 | 24 | | 2 (0.08) | 7 (0.29) | 8 (0.33) | 3 (0.13) | 4 (0.17) |

TP *T. penzigi*,; CM *C. mimosae*; CS *C. sjostedti*; CN *C. nigriceps; E empty/unoccupied*

Due to the take-overs, the abundance of *C. mimosae* gradually declined with time, while *C. sjostedti* increased (Fig 8.2). The number of unoccupied trees fluctuated with rainfall. For example, 1996 received low rainfall (Fig 3.2) resulted in a doubling of unoccupied trees in 1997, and after the 1997 rains, most of the unoccupied trees were colonised leaving less than 5% without ants.

### 8.4.3 Effect of ants on growth of *Acacia drepanolobium*

#### *8.4.3.1 Increase in Height and Diameter*

Increase in height and diameter of trees occupied by different ant species was similar. Among the ant species, mean growth in height of *A. drepanolobium* (Table 8.3) was greatest in trees with *C. mimosae* (26.0 cm), and lowest in *T. penzigi* (23.5 cm $yr^{-1}$). However, trees without any ant species had the lowest mean growth (17.2 cm $yr^{-1}$).

Table 8.3 Mean growth in cm ± (S.E.) in height and diameter of *Acacia drepanolobium* trees occupied by different ants over a 23 month period

| Ant species | Growth in height | Growth in diameter | Growth of twigs |
|---|---|---|---|
| *T. penzigi* | 45.1 ± 3.27 | 0.5 ± 0.03 | 8.0 ± 0.36 |
| *C. mimosae* | 49.9 ± 1.45 | 0.7 ± 0.01 | 7.5 ± 0.22 |
| *C. nigriceps* | 49.6 ± 3.10 | 0.7 ± 0.03 | 9.0 ± 0.30 |
| *C. sjostedti* | 46.4 ± 2.00 | 0.9 ± 0.02 | 7.2 ± 0.48 |
| Unoccupied | 33.0 ± 6.60 | 0.4 ± 0.05 | 5.4 ± 0.79 |

The ant species did not have a significant effect on growth in height of *A. drepanolobium* (ants nested with herbivore treatments in a random effect model, split plot design) (F= 0.85, P=0.67, df=24), but growth in diameter was significant (F=1.77, P=0.01, df=24). There was no significant interaction between ant species and herbivore treatments in the growth in height or diameter of *A. drepanolobium*, (F=0.70, P=0.83, df=20; F=0.75, P=0.76, df=20) for height and diameter respectively.

### *8.4.3.2 Twig lengths*

Data on the growth of twigs provided two insights. First, *C. nigriceps* had the greatest mean average twig growth and *C. mimosae* the least (Table 8.3). Mean twig growth was significantly different among trees occupied by different ant species. Secondly, *C. nigriceps* had the lowest maximum twig growth, 55 cm compared with 108 cm for both *C. mimosae* and *C. sjostedti*, while *T. penzigi* had 95 cm.

Table 8.4 Mean density per meter of twig length of new shoots, twigs, spines, and the mean length of spines most proximal to the second gall among *A. drepanolobium* trees occupied by different ant species

| Attribute / Treatment | Density of new shoots | Density of all twigs | Density of spines (pairs) | Spine length (cm) ''G'' |
|---|---|---|---|---|
| *T. penzigi* | 3.3 ± 0.13 | 7.1 ± 0.25 | 160.4 ± 5.07 | 1.7 ± 0.06 |
| *C. mimosae* | 2.9 ± 0.08 | 7.1 ± 0.14 | 149.3 ± 2.83 | 2.1 ± 0.06 |
| *C. nigriceps* | 4.0 ± 0.11 | 10.7 ± 0.21 | 162.3 ± 4.32 | 1.8 ± 0.05 |
| *C. sjostedti* | 3.0 ± 0.16 | 6.7 ± 0.30 | 140.3 ± 5.94 | 2.0 ± 0.07 |
| Unoccupied | 2.9 ± 0.30 | 7.8 ± 0.55 | 172.0 ± 11.11 | 1.9 ± 0.14 |

"G" spine most proximal to the second gall from the end of a shoot

The high mean recorded for *C. nigriceps* was more a consequence of no growth recorded on the sampled twigs occupied by the other species, rather than trees occupied by *C. nigriceps* having a greater growth. This also suggests that *C. nigriceps* had many but short new growing twigs (Table 8.4).

#### *8.4.3.3 Number of new growth points and density of twigs*

The number of new growing points per meter of twig/branch length ranged from 2.9 to 4.0, and was greatest in trees occupied by *C. nigriceps* and least in trees occupied by *C. mimosae* (Table 8.4). Mean differences in new growing points were significant (F=16.5, P<0.0001) among the ant species. *Crematogaster nigriceps* had significantly more new shoots than all the other species (P<0.05), while *T. penzigi* had more new growth points than either *C. mimosae* or *C. sjostedti*.

Most shoots on trees with *C. nigriceps* had numerous, short growths. These shoots had hardly elongated for more than two seasons. New growing shoots would then emerge in the next growing period. This pattern gave trees inhabited by *C. nigriceps* a unique physiognomy. Most of its branches were comprised of numerous but short internodes, and the canopy had a dense outlook. The canopy was denser, narrower and longer than those of the other ant species. These observations suggest that the ants modify the growth patterns of their host trees.

### 8.4.4 Canopy volume

Canopy volume was significantly different among the ant species (F=17.4, P< 0.0001), with *C. mimosae* recording the largest and *T. penzigi* the smallest. Canopy volume of the sampled trees increased with time (Fig. 8.3), suggesting bush encroachment was taking place by the thickening of the canopy layer.

The observed pattern reflects an increase in tree height, and a change of resident ant species. *Tetraponera penzigi* was expected to have the lowest canopy volume because it was more abundant among the smaller (shorter) than larger trees.

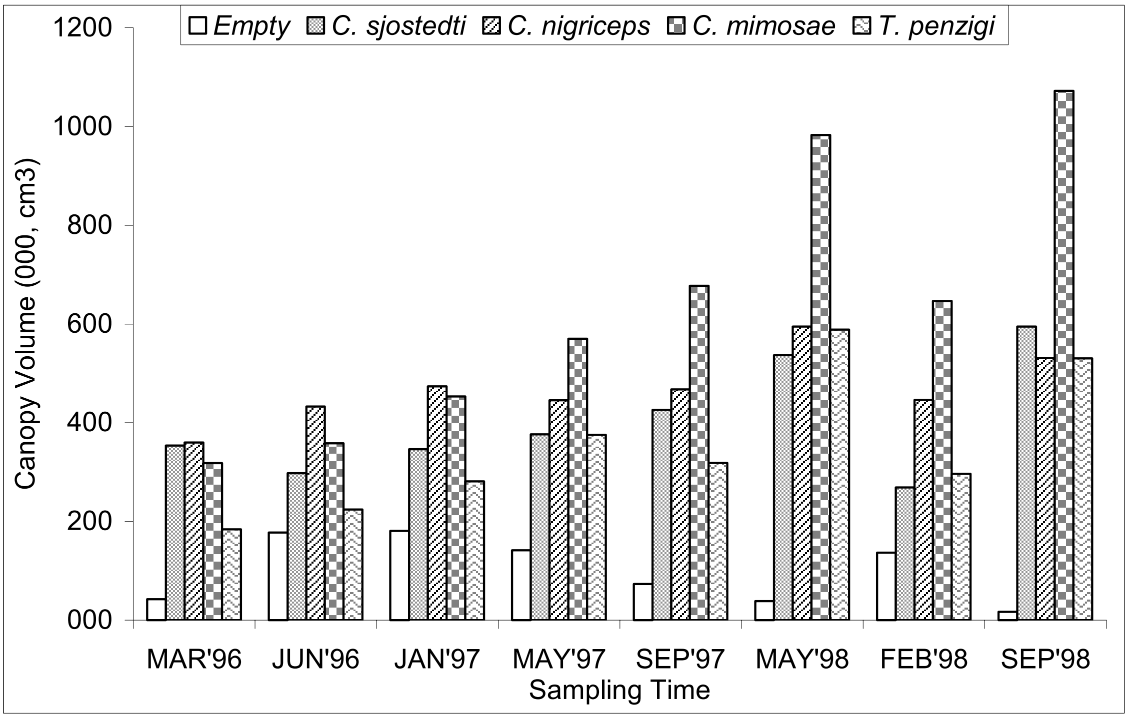

Fig. 8.3 Change in the canopy volume of *A. drepanolobium* over time.

Mean canopy volume was more a function of tree size than of the resident ant species. The preceding section showed that the size of a tree is to some extent a reflection of the ant occupant. Canopy height and mean crown diameter determine the canopy volume. For a similar height of tree, canopy height contributed more to canopy volume than did crown diameter. Canopy height was always greater for trees with *C. nigriceps* than *C. mimosae*, though the latter always had the greatest crown diameter.

### 8.4.5 Spine density and spine lengths

The mean spine densities were different (F=4.01, P=0.003) among the ant species (Table 8.4). Spine density fluctuated with time, but remained more or less unchanged between the start and end of data collection period. The spines of *C. nigriceps*-occupied trees were at a more acute angle (always less than $90^o$) and facing backwards when measured from the twig, compared to the almost right-angled ones of *T. penzigi*-occupied trees. Spines of trees occupied by *C. mimosae* and *C. sjostedti* were slightly more than $90^o$.

Mean lengths of spines most proximal to the second gall are presented in Table 8.4. Mean spine lengths were the converse of mean spine density, and were also significant (F=6.5, P=0.0001), a further evidence of the ants modifying their host trees. The mean lengths of spines at the distal end of the twig had a similar pattern, and similarly had significant differences among the ant species (F=2.9, P=0.02).

### 8.4.6 Gall density

Galls form on *A drepanolobium* trees in the presence or absence of ants. *Acacia drepanolobium* seedlings as young as 10 weeks (chapters 5 & 7) developed a few galls. The number of galls increased with tree size. Most of the galls are reddish grey and turn black when old. Some galls were found cracked open, but the cause of this was not apparent. Though primates (baboons and patas monkeys) were seen eating the gall contents, birds were also suspected of breaking the galls.

The galls of trees occupied by different ant species had subtle differences in shape and size. Galls on trees inhabited by *C. mimosae*, *C. sjostedti*, and *C. nigriceps* were bigger than galls on *T. penzigi* inhabited trees, and the diameters were different (F=3.31, P=0.03, df=5) (Table 8.5). Tukey-Kramer's HSD test showed that galls of *C. mimosae* occupied trees were significantly larger than those of *T. penzigi* (P=0.03). Galls of *T. penzigi* were rounder, and smaller (1-2.5 cm) with many small holes all over the gall. Galls of the *Crematogaster* species were large (2-4.2 cm) and the shape was similar to a cow's head. These galls had only two large holes, both at the confluence of the thorn and the gall.

Table 8.5 Mean diameters cm (± S.E.) of the most distal, the second most distal galls, and mean gall density (± S.E.) of *Acacia drepanolobium* trees occupied by different ant species. Mean diameters are based on a sample of 10 trees for each ant species, while mean density is based on samples of the KLEE experiment (Chapter Four)

| Ant species | Most distal gall | 2nd most distal gall | Gall density |
|---|---:|---:|---:|
| *T. penzigi* | 1.4 ± 0.07 | 1.7 ± 0.09 | 6.9 ± 0.14 |
| *C. mimosae* | 2.0 ± 0.11 | 2.6 ± 0.25 | 6.9 ± 0.12 |
| *C. nigriceps* | 1.9 ± 0.10 | 2.1 ± 0.24 | 8.1 ± 0.13 |
| *C. sjostedti* | 1.9 ± 0.22 | 2.3 ± 0.32 | 6.4 ± 0.17 |
| Unoccupied | - | - | 6.8 ± 0.42 |

Gall density varied with the resident ant species. Mean gall density was greatest in *C. nigriceps* (Table 8.5). This result is consistent with the observation of twig density, suggesting that with more new growth points per meter of twig, more galls are produced in trees occupied by *C. nigriceps*. *Acacia drepanolobium* may be responding to the presence and activities of different ant species by investing accordingly in twig growth, new twigs and galls.

### 8.4.7 Herbivory of trees occupied by different ants

The mean percentage of twigs browsed was greatest in trees occupied by *C. mimosae* (10.9% ± 0.30). Both *C. sjostedti* and *C. nigriceps* had similar percentages of their twigs browsed (10.6 ± 0.73 and 9.9% ± 0.44) respectively. The proportion of twigs on trees with *T. penzigi* browsed was low, (6.9% ± 0.45). The differences were significant (F=4.11, P<0.0001), *C. mimosae* and *T. penzigi* differing (P<0.05). This was attributed to *T. penzigi* being abundant on small sized trees, which were browsed least (chapter 4). Only a few twigs of unoccupied trees were used, which was also considered a consequence of more unoccupied trees being smaller and fewer, rather than a form of selective browsing. The interaction between ant species and herbivore treatment had a significant effect on utilization (F=4.07, P<0.0001). Trees in treatments with wildlife and mega-herbivores that were occupied by *C. sjostedti* were more browsed than trees in other treatment combinations.

Utilization of twigs fluctuated with the season among the ant species (Fig 8.4) that probably had more to do with animal movements and growing periods rather than the ant species. The levels of utilization suggest that browsers in this ecosystem probably do not differentiate between the ant species present, and may rely on other factors in choosing a tree to browse, a key one being size (chapter 4.3.4).

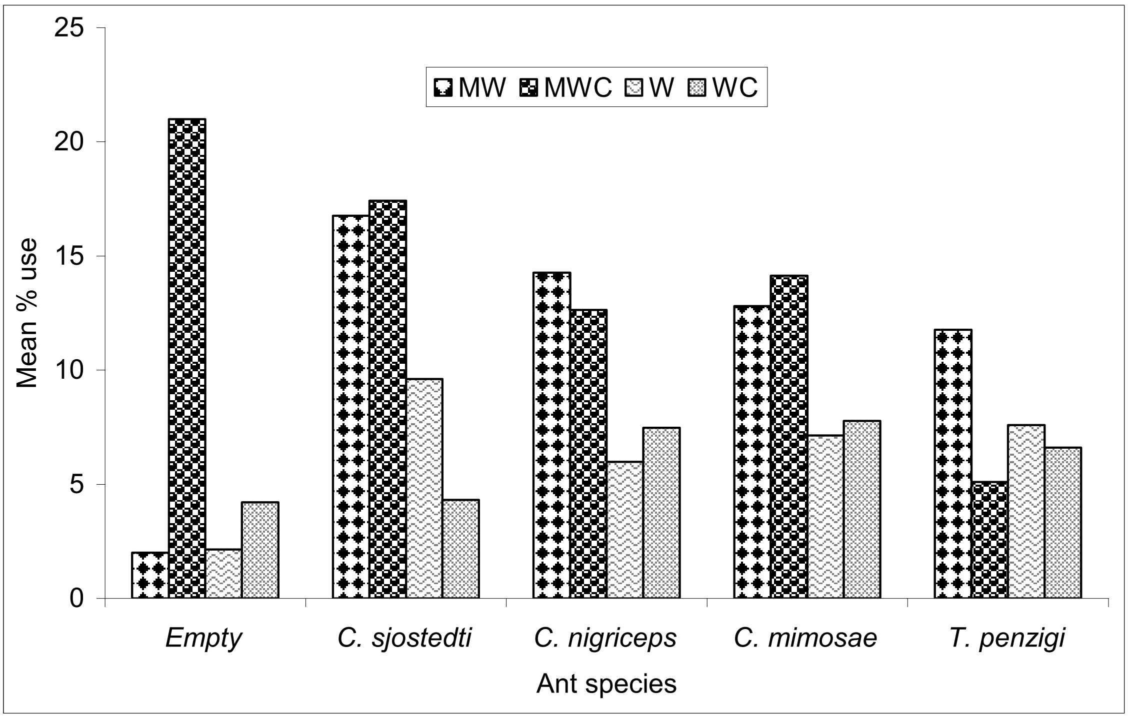

Fig. 8.4 Mean percent utilization of *A. drepanolobium* twigs over time on trees occupied by different ant species.

When data from treatments with mega-herbivores only were analysed, *C. sjostedti* occupied trees were the most browsed (17.4% ± 2.78) compared with 13.5% (± 0.59) and 13.4% (± .95) for *C. mimosae* and *C. nigriceps* respectively. Though Tukey-Kramer's HSD test did not pick any differences between these three ant species (P>0.05), the result suggests that mega-herbivores, specifically giraffes, could have opted for trees of the less belligerent *C. sjostedti* in preference to trees occupied by the other species.

### 8.4.8 Flowering and seed production

The probability of flowering was different among the ant species (Likelihood ratio $X^2$=343.2, P<0.001). It is more likely that *C. mimosae* and *C. sjostedti* occupied trees will be in flower. In a sample of 35 trees from the spray race site (5 km from KLEE), *Crematogaster mimosae* had 68.9% of its trees in flower, compared to only 5.8% in *C. nigriceps*. Flowering in *C. sjostedti* trees was similar to that of *C. mimosae* trees, but the latter were less abundant compared to the former. On the other hand, 43.2% of trees occupied by *T. penzigi* were in flower. When 600 trees from the mud-hole site (2 km from KLEE) were sampled, similar results were found (Fig 8.5).

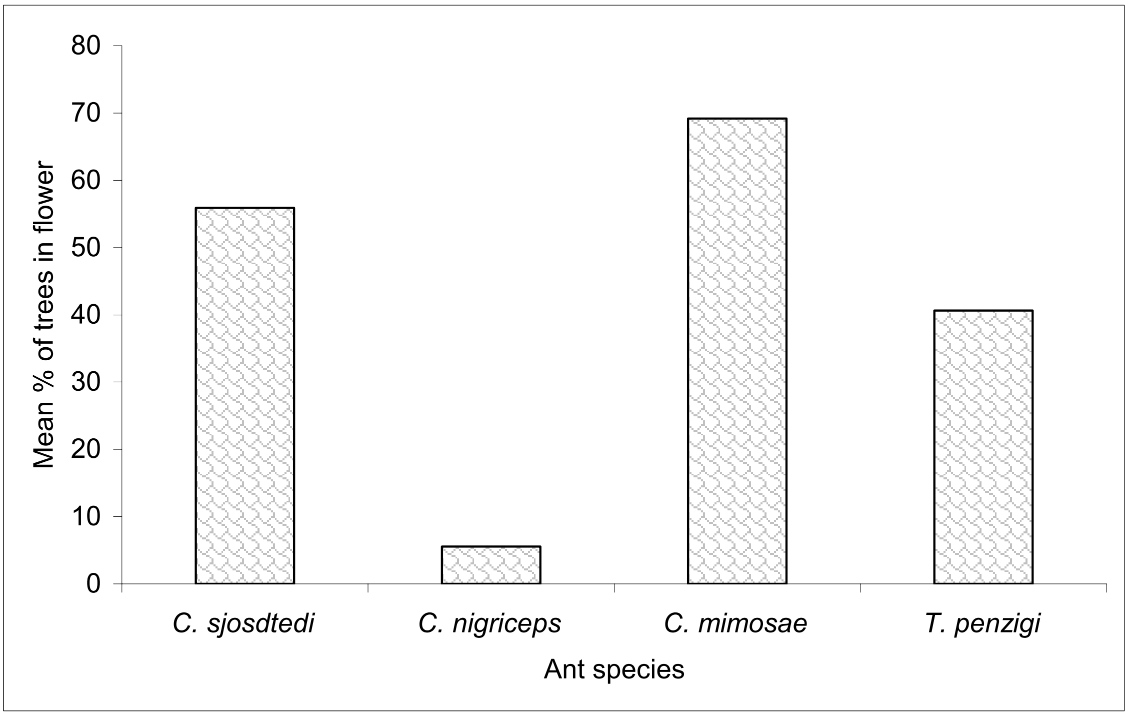

Fig. 8.5 Mean percent flowering of *A. drepanolobium* trees occupied by different ant species. N=630.

These results suggest that ant species play a big role in the fitness of a tree, which is ability of the tree to reproduce sexually. It is possible that all *C. nigriceps* occupied trees do not flower, and those recorded are due to ant take overs, especially from *T. penzigi* occupied trees.

### 8.4.9 Mortality of *Acacia drepanolobium* trees

Mortality was greatest in trees occupied by *T. penzigi* (9%) over the three-year period. Mortality in the other species was 4.6, 5.5, and 4.8% for *C. sjostedti*, *C. nigriceps* and *C. mimosae,* respectively. Trees that were unoccupied by any ant recorded 6.4% mortality. Most of the trees that died were below 50 cm in height, with a strong likelihood of being occupied by *T. penzigi* or unoccupied.

These smaller trees were susceptible to many forces of stress including trampling by herbivores, competition from grasses and bigger trees, and being eaten by ground-dwelling animals. There was no evidence to link the ant species to the observed mortality patterns.

## 8.5 DISCUSSION

### 8.5.1 Distribution and take-overs among ant species within *Acacia drepanolobium* community

*Crematogaster mimosae* was the most abundant *Acacia*-ant species, and *C. sjostedti* the least abundant in this ecosystem. Both *T. penzigi* and *C. nigriceps* were intermediate in abundance. The abundance of *C. mimosae* especially on bigger trees suggests that it is the dominant species on this tree in the Laikipia ecosystem. Young *et al*. (1997) also found *C. mimosae* to be the dominant ant on *A. drepanolobium* trees in a nearby *Acacia drepanolobium* woodland. Large trees are expected to have more resources than smaller ones because they have more galls, more leaves producing more extra-floral nectaries, more scale insects, hence more food. Hosting of these ant species and related insects significantly adds to the biodiversity of this ecosystem.

This state of four ant species on *A. drepanolobium* does not always repeat itself spatially over a wide area. At Mpala for example, there were stands of *A. drepanolobium* that had only *C. mimosae*, in which trees averaged 150 cm in height (see site 5 km away from KLEE, chapter 4). In the site 2 km away from KLEE, whose trees also had a mean height of 150 cm (range 65 - 270 cm), *C. nigriceps* occupied 41.5% and *C. mimosae* occupied 43.3 % of the trees. In Mkomazi Game Reserve in Northern Tanzania, Stapley (1998) reported that all the *A. drepanolobium* trees were occupied by *C. nigriceps* though she did not report the heights of trees surveyed.

The distribution and abundance of the *Acacia*-ant species may be spatially variable. This study has shown that composition and distribution of the acacia ants is temporally variable as a consequence of ant take-overs. This variability has significant implications for the interpretation of differences among ant species of the tree responses, and in most cases, confounds the response of the trees.

The abundance and distribution of the ant species seems to be associated with their individual behaviour. More belligerent species were generally more abundant than the less belligerent ones. Ant species vary in reaction to intrusion, *C. mimosae* and *C. nigriceps* responded rapidly to disturbance, and were belligerent, while *C. sjostedti* and *T. penzigi* were sluggish, and almost always had to be forced out of their swollen thorns. The most belligerent ants are not necessarily the most dominant, and the converse holds.

*Tetraponera penzigi,* the most actively colonising ant species, was most often found on small short (young) trees. The competitively dominant ants (*C. sjostedti* and *C. mimosae*) occupy almost all of the tallest and potentially oldest trees, while *C. nigriceps* occupies trees of intermediate size.

It is suggested that *C. sjostedti* is not abundant because it is a less belligerent species. It is also suggested that the abundance of *T. penzigi* is associated with its means of expansion by foundress queens, which may be less successful when it lands on trees that are already occupied by other ant species. Conversely, winged foundress queens will successfully establish colonies on unoccupied trees.

The near vertical distribution of the four species is intriguing. There is a possibility that some succession may be taking place, *T. penzigi* being the 'pioneer ant species' followed by *C. nigriceps*, with *C. mimosae* and *C. sjostedti* as 'climax' species. However, the ant take-overs suggest a more fluid situation. That take-overs were temporally variable suggest that succession is not the only factor at play.

The ant distribution among tree heights is probably the result of a contest for territory in the midst of a limited resource. The ant species try to dominate by taking over others' host trees, and thereby expand their colonies. The more aggressive and dominant ants are more likely to win such contests.

That *C. mimosae* was credited with most of the take-overs points to its dominance and greatly enhances its abundance. It also lost the least number of its host trees, suggesting its defensive superiority. *Crematogaster sjostedti* was second best to *C. mimosae* in acquiring new territories, but lost a substantial proportion of its trees. The probable explanation is that it is slow to react to intrusion, thereby making itself an easy target of take-overs, especially by the more aggressive and numerically abundant *C. mimosae,* which accounted for most of its lost trees. On the other hand, *T. penzigi* lost the greatest number of its host trees, and was a poor coloniser of occupied trees. Most of the trees *T. penzigi* acquired had previously been unoccupied, vindicating its mode of expansion (winged foundress queens), and suggesting that it engaged in fewer aggressive battles. *Crematogaster nigriceps*, like *C. mimosae,* lost few of its trees, suggesting that it can vigorously defend its territory. Most of its acquisition came from unoccupied trees as well. An ongoing study seeks to determine if *C. nigriceps* modifies its host tree in a manner that makes the tree less attractive to the other ants. Its quickness in reacting to disturbance may also be a factor in its ability to ward off intruding species.

Given the time period in which the take-overs took place, it is possible though unlikely, that some ants deserted trees, which, when vacant, were occupied by a different ant species.

Most of the unoccupied trees were short and small, less than 50 cm in height, and could have been empty as a result of the leaves drying out thus forcing the ants to migrate. These small trees had a small canopy volume, fewer 'galls' and therefore limited food reserves and shelter. The second means by which ants could have left (migrated) from trees was by the eating up of galls by baboons and patas monkeys, which left them with no galls to shelter in. Smaller trees were more susceptible because they had fewer galls, most of which were cracked open and all the brood eaten up by the primates. It is not yet known how a plant of a given height responds immediately to a take-over.

Nonetheless, the co-existence of these four ant species on the same plant species is of significant evolutionary importance, as it apparently contradicts the concept of competitive exclusion (Taper & Case 1992). Young *et al*. (1997) suggested four possible reasons for this:

i) Is the resource (*A. drepanolobium*) present in unlimited quantities?

ii) Niche separation and species succession;

iii) Succession and time lags and individual variability; and

iv) multiple-persistence states where it is difficult to dislodge *T. penzigi* and *C. nigriceps* (*T. penzigi* and *C. nigriceps* are destructive of their trees, make it easier to defend, and less attractive for invaders).

That the resource, *A. drepanolobium,* may be available in unlimited quantities is unlikely because few trees (less than 5%) were unoccupied. Most of the unoccupied trees were small-short trees, other unoccupied ones were dry or bereft of vegetation (a rare occurrence), or trees whose galls were cracked open. Most trees only became vacant after long dry spells. The fact that the four species fought for occupancy (territory) does not support the hypothesis of unlimited resources.

Secondly, to the extent that there is a specialised resource separation also has major caveats, though possible. It is possible in as far as information on the various attributes and characteristics of the resource are still lacking, and hence some specific but pertinent attributes may be unknown. However, the known characteristics are attributed to the presence of the ants themselves, and not changed by the trees as they age. All the four ant species were found in 'young' trees of less than 50 cm, and if any niche specialisation develops with age, it is unlikely that it would have been attained within such a ‘short’ time. However, the fact that all species were found in all the trees smaller than 390 cm confounds this line of reasoning. Given that the mean height of this tree over a wide range is 350 cm, and all the acacia ant species are found up to 390 cm discounts this line of argument.

Furthermore, it is highly improbable that these species would invest so much energy in ‘invading’ and ‘fighting’ for territories that are not suitable for them. It is suggested that the resource (*A. drepanolobium*) is finely uniform, and that the special ‘niches’ can only be created in the presence of ants, and these are not irreversible changes.

Is it possible that some kind of hierarchical succession takes place? The distribution of the ant species among the tree heights would seem to suggest this. The take-overs also support this hypothesis. It is apparent that if succession takes place, then the mode is not through facilitation The available evidence suggest that the modifications ascribed to the ant species (eating extra-floral nectaries dry for *T. penzigi*, eating of buds for *C. nigriceps*, and tending of scale insects for *C. mimosae* and *C. sjostedti*), are not of benefit to the succeeding ant species.

A question that begs is, which of *C. mimosae* and *C. sjostedti* forms the climax? The inclination has been to *C. sjostedti* (Young *et al*. 1997, Stanton M. L 1998[6], pers. comm.), although available evidence indicates that *C. mimosae* may be the ‘climax’ ant. Davidson & McKey (1993b), and Young *et al*. (1998) reported similar replacements through time in several myrmecophytes. It is also possible that both *C. sjostedti* and *C. mimosae* are climax species.

The succession hypothesis would imply that in mature stands, only *C. mimosae* and *C. sjostedti* would be the only ants presents. So far, there is no evidence to suggest this is the case. Instead, it is suggested that the occurrence of *C. mimosae* only in one of the seed production sites 5 km from KLEE, and that of *C. nigriceps* in Mkomazi (Stapley 1998) are not consistent with the succession hypothesis.

The multiple-persistence state is an attractive hypothesis given available quantitative evidence. It has been proved that no species lost more than half of it original host trees. Though this is a possibility with time, the available evidence suggests that the species

---

[6] Maureen L. Stanton, Mpala Research Centre, P. O. Box 555, Nanyuki, Kenya.

either modify their host trees to make them more defendable and less attractive to others or they have a greater competitive ability to colonise and more trees, or enhanced aggressiveness to defend their territories. There can be other reasons why the species co-exist on the same host.

Overall, *C. mimosae* is the dominant species and does not seem to affect the tree negatively, while at the same time offering differential protection against browsers. The browsers (e.g. elephants and giraffes) in turn have learnt to live with the ants (Madden & Young 1992).

Mutualistic relationships evolve to maximise the fitness of each partner separately (Janzen 1966). The adaptations that evolve are those favoured to maximise the overall reproductive success of individuals, independently of the effects of fitness of the other species. In some cases, the result may be that certain adaptations in one partner may be less than beneficial to the other, even when both will have overall benefits. It is also possible for parasites of these relationships to occur. It is possible for parasites to mimic the relationships and benefit from them. The case of *C. nigriceps* can be a subtle case of parasitism, where the ant gets full benefits (home and food), while stunting the growth of the plant, and in fact reducing its overall fitness by stifling flowering and seed production. However, by defending its home and food, it invariably defends the tree from herbivory.

Not all plant-ant relationships are alike, and the textbook paradigm of ant-plant mutualism may be oversimplified. A ‘joy ride’ hypothesis is suggested for the occurrence of the four mutually exclusive ants on the same homogeneous resource. In this hypothesis, it is proposed that *C. mimosae* co-evolved with the tree and the other ant species simply took advantage of the situation?

It is also suggested that the observed distribution and abundance is related with each species' aggressiveness, competitive and defensive ability, and the ability to colonise trees.

### 8.5.2 Effect of ants on growth

Trees occupied by *C. nigriceps* were expected to have a significantly lower growth rate because most twigs of the trees they occupied had short growths, and this would also be reflected on vertical growth. However, this was not the case, and growth was similar on all the trees occupied by the four ant species although trees with *T. penzigi* and *C. nigriceps* recorded slightly lower, but statistically insignificant growth.

Growth in twig lengths, though significantly different, showed that twigs on *C. nigriceps* occupied trees had shorter maximum growths. Most shoots on *C. nigriceps* trees looked vibrant and had more vigour, because they had more new shoots than trees occupied by other ant species. However, the overall physiognomy of *C. nigriceps* host trees looked sickly, as a result of many short dead or dry shoots. Given the short growths recorded on most of its trees, it is suggested that *C. nigriceps* actively suppresses growth of the twigs by removing the axillary buds, and that the tree responds by producing more new shoots. A question arising is whether this suppression is a deliberate modification of the tree physiognomy to suit *C. nigriceps*?

The reason(s) why *C. nigriceps* should modify the growth form of *A. drepanolobium* twigs are not quite apparent. There are a few possibilities. One hypothesis is that it modifies the growth of the tree to make it easily defendable. It is much easier to congregate many ants within a short time on shorter shoots than long ones. Secondly, because *C. nigriceps* feeds on axillary shoots, it needs many of them. As each axillary shoot is eaten up, the tree tries to put up more, all which are eaten up.

The growth patterns on the trees of the other three ant species do not suggest they modify its growth. However, the activities of these ants on the trees may indirectly influence growth patterns. For instance, *C. mimosae* tends scale insects, but the effect of this was not investigated. On the other hand, *C. sjostedti* allows other ants (*Camponatus* sp.) on its trees, and the possible effects were not investigated either. Finally, *T. penzigi* feeds on almost all the extra floral nectar produced by the tree. Is it possible that the tree allocates more resources to produce more extra floral nectar (to attract pollinators), and this has an indirect effect on growth?

### 8.5.3 Effect of ants on canopy volume

Canopy volume was significantly different among the ant species' hosts principally because of the differences in tree heights where each species is more abundant. Bigger trees occupied mostly by *C. mimosae* and *C. sjostedti* had greater canopy volume. However, the growth pattern of the canopies also had a role to play. The canopy heights of trees occupied by *C. nigriceps* tend to be longer than those occupied by other ants of similar size. Conversely, the canopy diameter of the former are smaller compared to the latter, and this is because of the modification in growth form discussed above.

A further consequence of the observed canopy volume is that trees occupied by *C. nigriceps* tend to be ‘bushier’ and 'denser' (more difficult to penetrate) than those of the other ant species. This bushiness is a consequence of the growth form of the twigs.

Closely related to canopy volume and twig growth is twig density. Density of twigs and new growth points were greater in trees occupied by *C. nigriceps*. This is also a consequence of the growth form these trees take.

More new growth points benefit *C. nigriceps* because more axillary shoots will grow, and it needs these for its food. This need was not observed on trees occupied by the other species.

By having more new growth points that do not grow very long, trees occupied by *C. nigriceps* do not grow as big a canopy as do trees occupied by the other ants of similar size. A consequence of this would be slower canopy growth than in the other species, but an increase in canopy density.

Though utilization was higher on trees with *C. mimosae*, it was fairly even among the ant species, and was low compared with utilization of other browse species (chapter 4). The differences in spine density among trees occupied by the four ants suggest differences in defence strategies. A possible reason for this may lie in the growth pattern of the twigs. Probably thorns grow on every node, but the inter node lengths were not investigated. It is probable that the density of spines per node would be similar.

The results on spine lengths also shed more light on the observed spine density. Spines on *C. mimosae* trees were longer than those in *C. nigriceps*, which were the shortest. Is it possible that once a tree has been modified to produce more spines, it will not invest much more in the length of the spine? The angle of inclination of the latter species trees suggests that they are adequately defended. As mentioned earlier, it was difficult to manoeuvre within the canopy of *C. nigriceps* occupied trees, and part of the reason was the angle of inclination of the spines. The longer spine lengths on the other ants’ trees suggest a different compromise in resource allocation, longer but fewer spines.

The ants also use spines as bridges to reach intruders. It is tempting to argue that a more vulnerable *C. nigriceps* would modify a tree to such an extent that it would be easily defended since it is aggressive enough. However, such a suggestion does not go well with *T. penzigi*, which is also vulnerable, had a high density but the shortest spine lengths. But a big question is, is it possible that *C. mimosae* needs longer spines to help it defend trees against herbivory?

Stapley (1998) reported that on trees occupied with *C. nigriceps*, ants and thorns on their own significantly reduced the amount of vegetation eaten on their branches compared to branches without them. She also added that the presence of either defence significantly increased the effectiveness of the other in reducing bite rates.

It is generally acknowledged that spines do not stop herbivory, but significantly reduce it (Young 1987). The presence of ants adds onto the existing defence strategy, making it more effective in limiting herbivory.

Density of galls was also similar to that of spine density. The implication here is that trees with *C. nigriceps* have more ants (assuming that each gall has the same number of ants). Galls are important in providing housing for the ants. Trees with more galls definitely provide a better environment for the ants than those that have less.

There is not enough evidence to suggest that the trees can increase or decrease the number of galls depending on the ant occupant. However, it is probable that the presence of different ants and their activities can modify how a tree allocates its resources. If ants are to be useful in limiting herbivory, then numbers are crucial, implying more housing is needed.

The galls are important for tending to the brood, and therefore propagation of a colony. They form a food base for primates like Patas monkeys and baboons. They are also crucial if a tree has to be colonised or re-colonised. Most unoccupied trees were short with damaged or broken galls, and the ants promptly moved on.

It should be noted that *C. sjostedti* were found in between tree barks, and some may even be living there. Indeed some of them were also found along the nearby Ewaso-Nyiro river, suggesting that they were not obligate ants. (Roy Snelling[7], pers com).

### 8.5.4 *Acacia* ants and herbivory

Except for *T. penzigi*, herbivory was similar among trees occupied by the dominant ant species. However the low levels of herbivory are consistent with enhanced defences against mammalian herbivory and the higher use recorded for non - *A. drepanolobium*

---

[7] Roy Snelling, Smithsonian Institution and Mpala Research Centre P O Box 555, Nanyuki, Kenya

trees, which are not defended by ants is indirect evidence of the role ants play in defence against herbivory.

The suite of factors that influence herbivory of *A. drepanolobium* shoots are many and compounded e.g. time or season and rainfall, affect movement of herbivores and food availability. Secondly, though foliage of *A. drepanolobium* is available almost all year round, the availability of forage from other species may determine to what extent *A. drepanolobium* foliage is utilized.

Fewer twigs of unoccupied and *T. penzigi* occupied trees were browsed, and this is believed to be related to the tree sizes involved. Evidence was availed in chapter 4 to this effect (shorter trees were browsed less than taller ones).

Another possibility for the seemingly uniform level of use among the dominant ant species could be the large diversity of mammalian herbivores, ranging from specialist browsers like giraffes to generalist browsers like Grant's gazelle. The results suggest an ant treatment effect, where browsers like giraffes probably browse more on trees with *C. sjostedti* than the other ant species.

Whether herbivores can discriminate between trees with different ant species was not investigated, and though these results suggest it, this seems highly unlikely. Using goats, Stapley (1998) reported that the amount of vegetation eaten from *A. drepanolobium* trees inhabited by *C. nigriceps* did not depend on the defence employed (thorns or ants). However, ants and thorns led to fewer bites.

A survey of twig utilization within the same ecosystem but which involved other browse species showed that herbivores browsed *A. drepanolobium* less than the other species, (*Cadaba farinosa, Rhus natalensis, A. brevispica, A. mellifera*, and *Balanites* sp). Of these species, only *C. farinosa* and *R. natalensis* are spineless. This indicates that the browsers preferred the trees without ants, leaving *A. drepanolobium*.

Therefore, the four ant species are important in limiting herbivory on *A. drepanolobium* by mammalian herbivores.

### 8.5.5 *Acacia* ants, flowering, seed production and mortality

Trees occupied by *C. mimosae*, *C. sjostedti*, and *T. penzigi* showed greater flowering and seed set compared with *C. nigriceps*. The implication is that *C. nigriceps* stifles flowering and therefore seed production in *A. drepanolobium*. It is probable that *C. nigriceps* action of eating axillary shoots and actually most of the fresh shoots on its host trees has a lot to do with the low flowering. It is thus suggested that *C. nigriceps* probably affects the fitness of *A. drepanolobium* negatively.

The implication is that *C. nigriceps* may be a parasite rather than a mutualist in this relationship, therefore suggesting that it could be one of the joy-riders in the plant-ant mutualism.

The mortality patterns suggest that resident ant species did not play a direct role in tree mortality. In any case, it would be to the benefit of the ants that their hosts lived for as long as possible. Though trees with *T. penzigi* recorded most of the deaths over the study period, this was more a consequence of the tree size than ant occupant. It was shown in chapter 4 that more smaller trees died than the larger ones, and the deaths ascribed to competition by grass, trampling by herbivores, and boring by beetles for the larger trees.

It was also observed that many shoots of *C. nigriceps* occupied trees dried out quicker than twigs from the other species, suggesting that this ant may have played a role in their deaths.

# 9 CHAPTER NINE: GENERAL DISCUSSION AND RECOMMENDATIONS

This chapter presents a summary of the major findings from the presented results and discussions. Recommendations for use in development and for future research are proffered.

The population dynamics of *Acacia drepanolobium* in the black cotton ecosystem is influenced to varying degrees by several factors acting singly or in combination. These factors include herbivory by different categories of herbivores, fire and harvesting. However, the study did not conclusively determine which of the investigated factors was the most critical in the observed dynamics.

## 9.1 FACTORS THAT INFLUENCE THE POPULATION DYNAMICS *OF ACACIA DREPANOLOBIUM* IN LAIKIPIA RANGELANDS

**Herbivory:** Results from this study show that herbivores are important in the population dynamics of the tree although *A. drepanolobium* was not the preferred browse species in the black cotton ecosystem of Laikipia studied, a fact that is ascribed to the relatively low density of known browsers like elephants and giraffes the study area. Herbivores present were important in influencing the population dynamics in the following ways:

1. Greater increase in shoot lengths for trees in plots where mega-herbivore and wildlife were allowed in – suggesting compensatory growth of the twigs.

2. The population of *A. drepanolobium* did not increase or decrease significantly with or without mega-herbivores during the study period; however, the greater mortality rates in mega-herbivore treatments is evidence that mega-herbivores were an important factor. Indeed studies in the Tsavo and Laikipia reported that presence of giraffes and elephants could lead to a reduction in overstorey population. Particularly in Laikipia, Moore (1974) reported a significant decline in *A. drepanolobium* population following intense browsing by elephants. In the period between 1992 and 1997, a rancher at Ol Jogi had to move giraffes out of a fenced park to allow for regeneration of *A. drepanolobium* trees. Hence, herbivores (mega-herbivores) when present in sufficient numbers can drive the population of *A. drepanolobium.* Birkett (2002) reported significant impacts on A. drepanolobium from mega-herbivores in a black rhino sanctuary within the Laikipia black cotton ecosystem, while the wildlife densities were significantly higher than the study site.

3. Absence of herbivores induced a decline in spinescence of *A. drepanolobium*. Although the importance of the reduction to the population dynamics was not investigated, it can be hypothesised that more resources (usually spent on spinescence) could be directed to other fitness factors. Theoretically, this observation adds credence to the growing body of evidence that spines are a herbivory reduced phenomenon in some plants. However, the extent to which exclusion of herbivory can reduce spinescence of African acacias cannot be easily extrapolated. There is no likelihood that all spines in the trees will totally disappear in the absence of herbivory.

**Fire:** Fire is a ubiquitous phenomenon in most savanna ecosystems was identified as a major factor that influenced the dynamics of *A. drepanolobium* woodlands although it did not kill any trees under investigation. Rather, fire is important in seed germination, wiping out fire susceptible shrubs e.g. *Cadaba farinosa*, and triggering flowering of important understorey species like *Themeda triandra* and *Lintonia nutans*. The burning also resulted in a significant improvement in the nutrient status of the herb layer species.

Fire is thus an important tool for management of *A. drepanolobium* woodlands. For one, it helps to clear the brush and open the range for grazing; Secondly, it kills seeds of *A. drepanolobium* thereby preventing regeneration through seed; Thirdly, it kills other woody species thereby controlling bush encroachment; Fourthly, it can alter the species composition of the herb layer species, in this case from the less palatable *Pennisetum* sp. to the preferred *Themeda triandra*; Fifthly, fire improved the nutrient status of the herb layer species.

**Harvesting:** The act of harvesting trees for fuelwood production and other uses sets in motion intra-system dynamics. Chrono-sequence regrowth estimates showed that *A. drepanolobium* can grow to maturity within 14 years of harvesting. Regrowth is through coppicing, with the number of coppice material reduced with each subsequent year, leaving one or two dominant stems/trunks by the 12th year. Re-growth and coppicing are aggressive, while factors that hindered the proliferation of other woody species were not well investigated. This suggests that within the black cotton ecosystem, *A. drepanolobium* has a distinct comparative advantage over other trees and shrubs.

Importantly too, is the fact that harvesting of *A. drepanolobium* for fuel-wood is a sustainable management practice that also influences its population dynamics. When the trees are harvested, flowering cannot take place at least until three years later.

For management of *A. drepanolobium* woodlands, planned and scientific harvesting of charcoal is a very appropriate tool. Together with the use of fire, harvesting for charcoal also adds on to the income of ranching enterprises.

***Acacia* Ants**: Four acacia ant species (*C. mimosae, C. sjoestedti, C. nigriceps*, and *T penzigi*) were found to be ubiquitous within *A. drepanolobium* trees. These ants occupy the trees in a mutually exclusive pattern. Results from this study suggest that the ants influenced to a significant extent, growth and flowering patterns of *A. drepanolobium*.

Trees occupied by *C. nigriceps* had a significantly different physiognomy compared with those occupied by the other ant species. Secondly, trees occupied by this ant did not flower. The size and shape of the galls on trees occupied by these ants also differed. It can be deduced that *Acacia* ants can influence the population dynamics of *A. drepanolobium* depending on the ant species occupying a tree, and the factors that drive or determine the colonization and take-over dynamics.

Though at the outset the study was not designed to investigate the effects of these ants on the tree's population dynamics, these observations point to a significant role played by these ants on *A. drepanolobium* population dynamics. These effects should be further investigated.

Other factors influencing *A. drepanolobium* population dynamics:

a) Bruchid beetles were important in the rates of *A. drepanolobium* seed germination. Because germination is a critical phase of plant population dynamics, and factors affecting it significantly influence the overall dynamics.

b) Climate, especially rains are important in photosynthesis. In *A. drepanolobium*, growth of the trees, twigs and flowering are dependent on rains.

c) The study species is found almost exclusively in black cotton soils. Where-as the study did not investigate factors in the soil that give *A. drepanolobium* a comparative advantage over other trees and shrubs, the observed gradient in its density as the soil clay content changes points to soil as an important factor.

## 9.2 IMPORTANT PHASES IN THE LIFE CYCLE OF *ACACIA DREPANOLOBIUM*

**Seed:** Seeds are the most important phase in the propagation of most plants. The same applies to *A. drepanolobium* in Laikipia. Seeds of this tree are dehiscent, can be dispersed by wind, water and herbivores. However, their susceptibility to bruchid beetles and fires are critically important factors in the population dynamics of the tree. Both bruchid beetles and fire significantly reduce the germination rates of *A. drepanolobium* seeds.

Flowering: Within the KLEE sites, flowering was minimal with the consequence that very few seedlings emerged during the study period. Factors that influence flowering were not investigated, however, this study has conclusively shown that flowering was dependent on the ant species occupying the tree, and specifically that tree occupied by *C. nigriceps* did not flower.

Seedlings are an important phase in the population dynamics of *A. drepanolobium* in several ways. First, it is seedlings that establish to become the trees, and therefore their survival is important for effective natural replacement of dead trees. This study has shown that the growth of seedlings was affected by the amount of grasses, herbivory and fire. Fire in particular defoliates the seedlings, thus significantly impacting on growth and establishment.

Tree size: It is only from mature trees that flowering and hence seed production takes place. Browsing was greater in bigger (mature) trees compared with smaller ones. The number of galls, and therefore *Acacia* ants was largely a function of tree size because bigger trees had more galls. Bigger trees grew faster (especially canopy volume) and are thus very important in its population dynamics. This study has shown that seed production was related to the tree size.

## 9.3 BUSH ENCROACHMENT BY *ACACIA DREPANOLOBIUM* FROM A POPULATION DYNAMICS PERSPECTIVE

Bush encroachment by *A. drepanolobium* in the ecosystem under study has two significant attributes; factors that seem to encourage encroachment and those that stifle encroachment.

Among important attributes that encourage bush encroachment in Laikipia are low rates of herbivory, high rates of seed germination, relatively fast rates of growth, ability to coppice, and adaptation to fire.

Among factors that seem to control bush encroachment in *A. drepanolobium* are bruchid beetles that affect seed germination, low flowering rates, *acacia* ants that stifle flower and pod production, and fires that kill seeds and reduce germination.

From the perspective of population dynamics, *A. drepanolobium* holds encroachment potential. In this ecosystem, it is actually a bush problem. However, management can intervene by using fires (which will reduce germination), and harvesting, which has additional economic benefits if the trees are used for fuel-wood.

## 9.4 SCIENTIFIC SIGNIFICANCE OF THE FINDINGS

This study has shown that population dynamics were useful in obtaining insights into the biology of *A. drepanolobium*, and some of the factors that influence it. The role played by herbivores on the population dynamics was not conclusive. On the other hand, the limited fire experiments clearly show that fire can have profound effects on the population dynamics of the tree.

A flow model is proposed that shows how the different factors studied can influence the population dynamics of the tree (Fig. 9.1). The main components of the model that determine the dynamics are fire, rainfall and management. Management refers to the use of different tools and systems to achieve a desired objective, e.g. browsers can be used to stifle browse production depending on their density. Management can also choose when to use fire to influence the dynamics in the range.

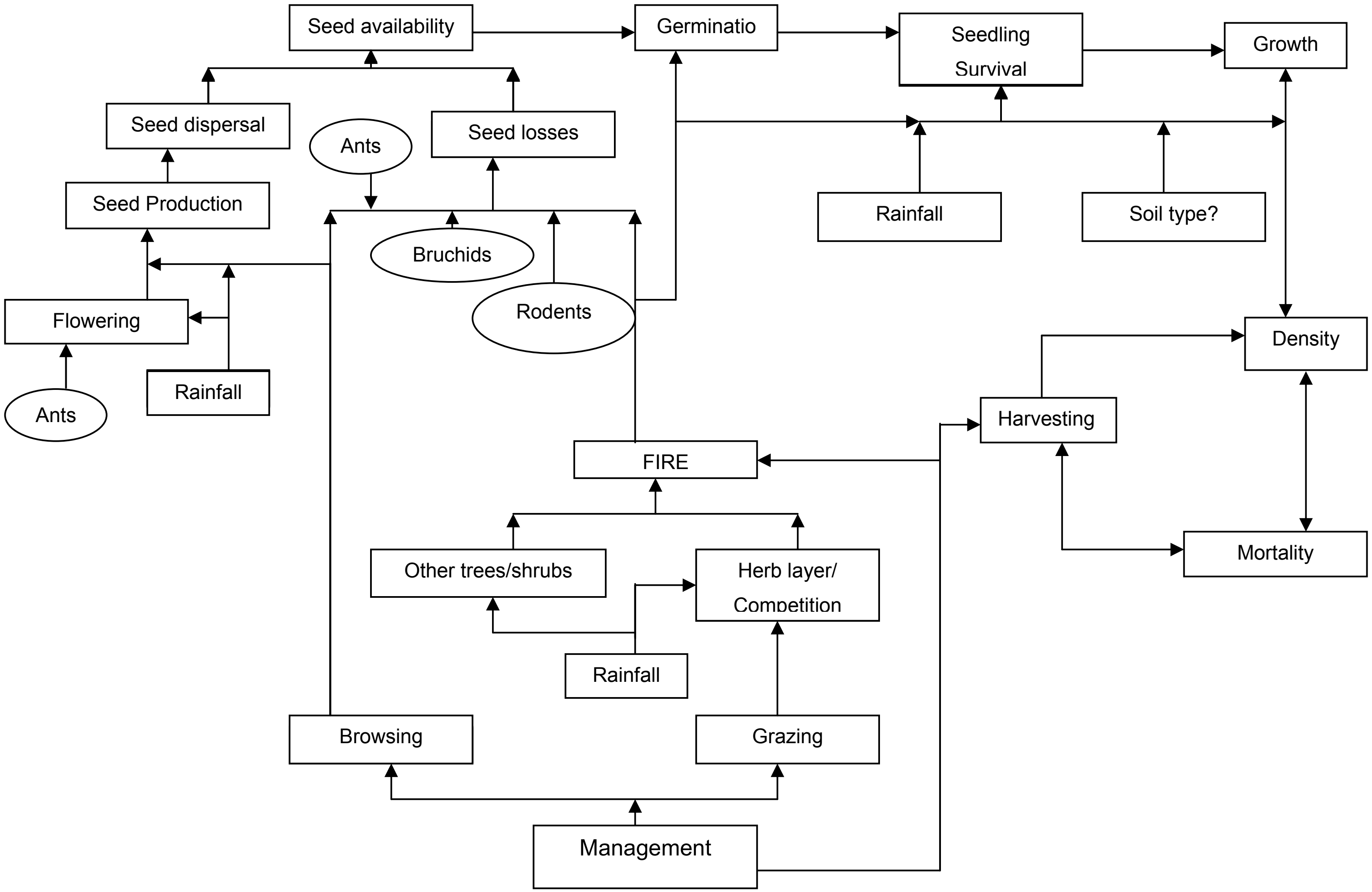

Fig. 9.1Flow diagram of ecological factors that drive the population dynamics of *A. drepanolobium*

Fires, whether natural or management induced are the most potent form of defoliation in the range, and affect many ecological processes e.g. killing seeds of some species, killing some plant species, enhancing germination of some species, releasing tied up nutrients in plants e.g. phosphorus, reducing competition for space and nutrients among others (Deshmukh 1986). Rainfall on the other hand is critical for many physiological processes within the plants to take place starting from photosynthesis, flowering and seed production, to growth and survival.

## 9.5 DEVELOPMENT OPTIONS FROM THE STUDY

- Many ranchers/farmers with *A. drepanolobium* on their property had alleged that *A. drepanolobium* is a problem tree. Though the study did not investigate whether *A. drepanolobium* was spreading into new territories, there is ample evidence that 1) it is mainly restricted to the black cotton soils, 2) some have expanded into red soils underlain by black cotton soils, 3) some *A. drepanolobium* trees have invaded hitherto glade areas within the black cotton soils, 4) there is a possibility that the density of the tree within the black cotton *A. drepanolobium* woodlands, has increased.

Arising from the results presented in the earlier chapters, it is suggested that managers and property owners can:

- Manage the *A. drepanolobium* woodlands by prescribed fire. Though the study did not show any *A. drepanolobium* deaths by burning, fire kills seeds of the tree thereby preventing regeneration from seed, clears the brush and improves accessibility to livestock, and also results in an overall improvement in the nutrient status of the herb layer.

Managers should design a fuelwood-harvesting programme either for firewood or charcoal and thereby get additional income. Harvesting of *A. drepanolobium* for use as source of fuel wood and timber (paper industry) on a cycle of 10-15 years. In which case, clear felling will be appropriate. The debris can be used to reclaim denuded parts by covering them with twigs.

- Keep large densities of browser animals, which will, over time, biologically control bush cover and spread of the tree.
- Other uses of *A. drepanolobium* that can be explored include the use of its spines (e.g. as toothpicks after treatment), and the use of its galls for decorations.

- In times of need, the leaves can be harvested and used as forage after the ants have been removed.

## 9.6 RECOMMENDATIONS FOR FURTHER RESEARCH

- The results on how herbivores influence the population dynamics of *A. drepanolobium* were not conclusive on several fronts. It is suggested that this experiment be continued to determine the long term effects.
- Flowering was very minimal during the study period. It is suggested that an experiment be designed to determine the factors that influence flowering of *A. drepanolobium* in this environment.
- An important aspect of *A. drepanolobium* trees, that was not investigated, is why different sites with the Laikipia plateau have stands of different maximum heights. Is this difference caused by soils or rainfall?
- Factors that led to, or influenced, mortality of the tree were not investigated. Though the beetle *C. dorsata* was suspected of weakening the trees, there is a need to investigate this further to establish beyond doubt, its role in the mortality of the trees. Further, its relationship with the wasp should also be investigated.
- The observations on the *Acacia* ants raised several questions. Although there are on-going studies about the relationship between the trees and the ants, the role of the ants on the growth and flowering of the tree should be given special attention.
- The effect of fire on the population dynamics of the woodland should also be investigated for a much longer time. Land and resources allowing, the fire experiment should be taken to the next level to examine the effects of fire type, season, frequency and intensity on the population dynamics of *A. drepanolobium*. Interactions between fire, grazing and browsing should also be studied focusing on the herb layer and dynamics in *A. drepanolobium*
- Other economic uses for this tree species.

# LITERATURE CITED

5th National Development Plan, 1986. Government of Kenya, 1987-1993, Government Printer, Nairobi, Kenya.

Agnew, A. D. Q. & Agnew, S. 1994. Upland Kenya wildflowers. East African Natural History Society, Nairobi.

Ahn, P. M. & Geiger, L. C. 1987. Soils of Laikipia District. National Agricultural Research Laboratories, Nairobi, Kenya.

AOAC, 1980. *Official Methods of Analysis*, 13th edition (Horwitz W, ed.). Association of Official Analytical Chemists, Washington D. C.

Ayuko, L J, 1978. Management of Rangelands in Kenya to increase beef production: socio-economic constraints and policies, proceedings of international range congress 1: 82-86.

Back, P. V. 1998. Control of currant bush (*Carissa ovata*) in developed briglow (*Acacia harpophylla*) country. Tropical Grasslands. 32: 259-263.

Barnes, R. F. W. 1990. Deforestation trends in tropical Africa. African Journal of Ecology. 28: 161-173.

Baumer, M. 1990. The potential role of Agroforestry in combating desertification and environmental degradation; with special reference to Africa. Technical Center for Agricultural and Rural Cooperation, Wageningen, Netherlands.

Baxter, B. J. M., Van Staden, J., Granger, J. E. & Brown, N. A. C. 1994. Plant-derived smoke and some extracts stimulate seed germination of the fire-climax grass *Themeda triandra*. Environmental and Experimental Botany 34: 217 – 223.

Beentje, H. 1994. Kenya Trees Shrubs and Lianas. National Museums of Kenya.

Behnke R. B. & Scoones, I. 1992. Rethinking range ecology: Implications for rangeland management in Africa. IIED Publications – 7282IIED.

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

Belsky, A J 1990. Tree grass ratios in East African savannas: A comparison of existing models. Journal of Biogeography. 17: 483-489.

Belsky, A. J. 1994. Influence of trees on savanna productivity: Tests of shade, nutrients, and tree-grass competition. Ecology 75. 53-59.

Belsky, A. J. 1995. Spatial and temporal landscape patterns in arid and semi-arid African savanna. In: L. Hanson, L. Fahrig & G Merriam (eds.) Mosaic landscapes and ecological process. pp 31-56. Chapman & Hall, New York.

Ben-Shakar, R. 1991. Abundance of trees and grasses in a woodland savanna in relation to environmental factors. Journal of Vegetation Science. 2: 645-350.

Birkett, A. 2002. The impact of giraffe, rhino and elephant on the habitat of a black rhino sanctuary in Kenya. African Journal of Ecology. 40: 276-282.

Bock, C. E., Bock, J. H., Grant, M. C. & Seastedt, T. R. 1995. Effects of fire on abundance of *Eragrostis intermedia* in a semi-arid grassland in south-eastern Arizona. Journal of Vegetation Science 6: 325-328.

Bogdan, A. V.1958. A revised list of Kenya grasses (with keys for identification). Government Printer, Nairobi.

Bonham, C. D. 1989. Measurements for terrestrial vegetation. John Wiley & Sons. New York.

Boo, R. M., Pelaez, D. V., Bunting, S. C., Elia, O. R. & Mayor, M. D. 1996. Effect of fire on grasses in central semi-arid Argentina. Journal of Arid Environments. 32: 259-269.

Boonman, J. G. 1993. East Africa's Grasses and Fodders: Their ecology and husbandry. Kluwer Academic Publishers.

Booysen, D. & Tainton N. M. 1984. Ecological effects of fire in South African ecosystems. Springer Verlag, New York.

Bourliere, F (ed). 1983. Ecosystems of the World 13. Tropical Savannas. Elsevier, Amsterdam.

Bradley, P. N. 1988. Survey of woody biomass on farms in Kenya. Ambio. 17: 40-48.

Brewer, J. S. 1995. The relationship between soil fertility and fire-stimulated floral induction in two populations of grass-leafed aster, *Pityopsis grammifolia*. Oikos 74: 45-54.

Brewer, J. S. & Platt, W. J. 1994. Effects of fire and herbivory on reproductive success in a clonal forb, *Pityopsis grammifolia.* Journal of Ecology 82: 665-685.

Brower, J. E., Zar, J. H. & Van Ende, C. N. 1990. Field and laboratory methods for General ecology. W. C. B. publishers IOWA.

Brown, J. R. & Carter, J. 1998. Spatial and temporal patterns of exotic shrub invasion in an Australian tropical grassland. Landscape Ecology. 13: 93-102.

Brown, J. R., Scanlan, J. C. & McIvor, G. 1998. Competition by herbs as a limiting factor in shrub invasion in grassland: A test with different growth forms. Journal of Vegetation Science. 9: 829-836.

Bryant, J. P., Chapin, III F. S., & Klein, D. R. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40: 357-368.

Bryant, J. P., Kuropat, P. J., Cooper, S. M., Frisby, K. & Owen-Smith, N. 1989. Resource availability hypothesis of plant anti-herbivore defence tested in a South African savanna. Nature: 227-229.

Buech, R. R. & Rugg, D. J. 1989. Biomass relations of shrub components and their generality. Forest Ecology and Management. 26: 257-264.

Butterworth, M. H. & Lambourne, L. J. 1985. Productivity improvement and resource conservation in the use of African rangelands. Rangelands, a Resource Under Siege. Joss P. J, Lynch PW, and Williams O B. (eds.) pp 111-114.Cambridge University Press.

Cannel, M. G. R. 1983. Plant management in agroforestry: Manipulation of trees, densities, and mixtures of trees and herbaceous crops. In: Plant Research and Agroforestry (Ed. P. A Huxley), ICRAF, Nairobi- Kenya.

Caughley, G. 1986. Rangelands, livestock and wildlife, the ecological equivalent of sulphur, saltpetre and charcoal. Rangelands, a Resource Under Siege. Joss P. J, Lynch PW, and Williams O B. (eds.). pp 545. Cambridge University Press.

Cavanagh, A. K. 1980. A review of some aspects of the germination of *Acacia*: Proceedings of the Royal Society of Victoria. 9: 161-180.

CBS (Central Bureau of Statistics), 2000. National population and housing census 1999. Ministry of Planning. Government Printer, Nairobi.

CBS (Central Bureau of Statistics), 2005: Population Estimates. Government Printer, Nairobi Kenya.

Chidumayo, E. N. 1978. Woodland structure, destruction and conservation in the copper belt area of Zambia. Biological Conservation. 40: 89-10.

Christensen, N. L. 1997. Managing for heterogeneity and complexity on dynamic landscapes. In: Pickett et al. (eds.). The Ecological Basis of Conservation pp167-186. Chapman & Hall New York.

Coe, M. 1993. The *Acacia* tree, a symbol of Africa. African Wildlife. 27: 75-77.

Coe, M., & Beentje, H. 1991. A field guide to the *Acacia* of Kenya. Oxford University Press, London.

Coe, M. & Coe, C. 1987. Large herbivores, Acacia trees, and bruchid beetles. South African Journal of Science. 83: 624-635.

Coley, P. D., Bryant, J. P., & Chapin, F. S. 1985. Resource availability and plant anti-herbivore defence. Science 230: 895-899.

Cooper, S. M. & Owen-Smith, N. 1986. Effects of plant spinescence on large mammalian herbivores. Oecologia 68: 446-455.

Coppock, D. L. 1990. Bush control: Opportunity for resource management and pastoral income generation? ILCA Newsletter 9: (13) 10-11. ILCA, Addis Ababa.

Coppock, D. L. 1994. The Borana plateau of Southern Ethiopia: Synthesis of pastoral research, development and change 1080-1991. ILCA, Addis Ababa.

Cunningham, P. L. 1996. Prospects for sustained harvesting of mopane (*Colophospermum mopane*) on the Venetia Limpopo nature reserve and its implications for browsing ungulates. MSc. Thesis, University of Stellenbosch.

D'Odorico P., Laio F., & Ridolfi L. 2005. A probabilistic analysis of fire-induced tree-grass coexistence in Savannas. The American Naturalist 167: (3) 79-87.

Davidson, D. W., & McKey, D. 1993a. Ant-plant symbioses: Stalking the Chuyachaqui. Trends in Ecology and evolution 8: 326-332.

Davidson, D. W., & McKey, D. 1993b. The evolutionary ecology of symbiotic ant-plant relationships. J. Hymenoptera Research 2: 13-83.

Deshmukh, I. 1986. Ecology and Tropical Biology. Blackwell Scientific Publications, Inc. California.

Deshmukh, I. 1992. Estimation of wood biomass in the Jubba Valley, southern Somalia, and its application to East African rangelands. African Journal of Ecology. 30: 127-136.

Dorgeloh, W. G. 1999a. Chemical quality of the burnt and non-burnt grass layer in the Nylsvlei Nature Reserve, South Africa. African Journal of Ecology. 37: 168-179.

Dorgeloh, W. G. 1999b. Diversity of the herbaceous layer in mixed bushveld. Journal of Range Management. 52: 519-524

Dorst, J. & Dandelot, P. 1972. A field guide to the larger mammals of *Africa*. Collins, London.

DRSRS (Department of Remote Surveys and Remote Sensing), & Mpala Research Center 1998. Laikipia wildlife counts.

Dregne, H. E. 1986. Desertification of arid lands. Advances in Desert and Arid Land Technology and Development. Vol 3. NY. Harwood.

Du Toit, J. T. 1990a. Feeding height stratification among African browsing ruminants. African Journal of Ecology. 28: 55-61.

Du Toit, J. T. 1990b. Giraffe feeding on *Acacia* flowers: predation or pollination? African Journal of Ecology. 28: 63-68.

Dublin, H. T. 1991. Dynamics of the Serengeti-Mara woodlands: An historical perspective. For. Conservation History. 35: 169-178.

Dublin, H. T. 1995. Vegetation dynamics in the Serengeti-Mara ecosystem: the role of elephants, fire and other factors. In: Sinclair A. R. E. & Arcese P. Serengeti II. Dynamics, Management, and Conservation of an Ecosystem pp 71-90. Chicago University Press. Chicago.

Edroma, E. L. 1981. The role of grazing in maintaining high species composition in *Imperata* grassland in Ruwenzori National Park, Uganda. African Journal of Ecology. 19: 215-233.

Edroma, E. L. 1984. Effects of burning and grazing on the productivity and number of plants in Queen Elizabeth National Park, Uganda. African Journal of Ecology 22: 165-174.

Edroma, E. L. 1985. Effects of clipping on *Themeda triandra* Forsk and *Brachiaria platynota* (K. Schum) Robyns in Queen Elizabeth National Park, Uganda. African Journal of Ecology. 23: 45-51.

Eltringham, S. K. 1976. The frequency and extent of uncontrolled grass fires in Ruwenzori National Park, Uganda. East African Wildlife Journal. 14: 215-222.

Eshete, G. & Stahl, G. 1999. Tree rings as indicators of growth periodicity of *Acacia* in the Rift valley of Ethiopia. Forest Ecology and Management 116: 107-117.

Estes, R. D. 1991. The behaviour guide to African mammals. University of California Press, Berkeley.

Fagg, C. W. & Stewart, J. L. 1994. The value of *Acacia* and *Prosopis* in arid and semi-arid environments. Academic Press. New York

FAO (Food and Agricultural Organisation), Report 1996. The present state of fragile ecosystems in dry lands and the role of forestry in their restoration. International Expert Meeting on Rehabilitation of Degraded Forest Ecosystems, Lisbon 24-28 June 1996.

Fenner, M. 1986. Seed ecology. Chapman and Hall, London.

Georgiadis, N. J & McNaughton, S. J. 1990. Elemental and fibre contents of savanna grasses: variation with grazing, soil type, season and species. Journal of Applied Ecology. 27. 623-634.

Georgiadis, N. J, Olwero, N. & Ojwang, G. 2003. Numbers and distributions of large herbivores in Laikipia District, Leroghi and Lewa Conservancy. Sample count, February 2003. Laikipia Wildlife Forum, Nanyuki, Kenya.

Giannoni, S. M., Borghi, C. E, Dacar, M. and Campos, C. M. 2005. Main food categories in diets of Sigmodontine rodents in the Monte (Argentina). Mastozoologia Neotropical. 12: 181-187.

Gichohi, H., Mwangi, E., & Gakahu, G. 1996. Savanna ecosystems. In: McClanahan T. M. & Young T. P. (eds.). East African Ecosystems and their Conservation. Oxford University Press, NY, pp 273-298.

Government of Kenya, 2004. ERS (Economic Recovery Strategy Paper for Growth and Wealth Creation). Government Printer, Nairobi Kenya.

Grootenhuis, J. G. 1990. Disease research for integration of livestock and wildlife. IN: Grootenhuis J. G., Njuguna S. G., & Kat P. W. 1990 (eds.). Wildlife Research for Sustainable Development. Pp 97-106. KARI, KWS & NMK.

Grootenhuis, J. G., Njuguna, S. G., & Kat, P. W. 1990 (eds.). Wildlife Research for Sustainable Development. Pp 97-106. KARI (Kenya Agricultural Research Institute), KWS (Kenya Wildlife Services) and NMK (National Museums of Kenya).

Halevy, G 1974. Effects of gazelle on seed beetles (Bruchidae) on germination and establishment of *Acacia* species. Israeli Journal of Botany. 23: 120-126.

Haro, G. O. & Oba, G. 1993. Dynamics of *Acacia tortilis* litter in the Turkwel River floodplain woodlands, Kenya. African Journal of Ecology 31: 200-209.

Harper, J. L. 1977. Population biology of plants. Academic Press New York.

Harrington, G. N. & Ross, I. C. 1974. The savanna ecology of Kidepo Valley National Park: The effects of burning and browsing on the vegetation. East African Wildlife Journal. 12: 93-105.

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, H. F. 1960. Range Management in East Africa. Government Printer, Nairobi.

Heady, H. F. 1966. The influence of grazing on the composition of *Themeda triandra* grassland, East Africa. Journal of Ecology 54: 705-727.

Heady, H. F 1978: Rangeland Management. John Wiley and Sons.

Heady, H. F & Heady, E. B. 1982. Range and Wildlife Management in the tropics. ITA Series. Longman.

Herlocker, D. J. 1996. Rangeland degradation in arid and semi-arid East Africa. In McClanahan T. M., and Young T. P. (eds.). East African Ecosystems and their Conservation. Oxford University Press, NY pp 266-267

Herlocker, D. J. 1999. Rangeland Resources in Eastern Africa: Their Ecology and Development. GTZ Nairobi.

Higgins, S. I., Richardson, D. M., Cowling, R. M. & Trinder-Smith, T. H. 1999. Predicting landscape-scale distribution of alien plants and their threat to plant diversity. Conservation Biology. 13: 303-313.

Hobbs, R. J. & Grimmingham, G. H. 1987. Vegetation, fire and herbivore interactions in heathland. Advances in Ecological Research. 16: 87-158.

Hocking, B. 1970. Insect associations with the swollen thorn *Acacia*. Trans. R Entomological Society of London. 122: 211-255.

Hodgkinson, K. C. & Harrington, G. N. 1985. The case for prescribed burning to control shrubs in Eastern semi-arid woodlands. Australian Rangeland Journal. 7: 64-74.

Hodgkinson, K. C. 1986. Responses of rangeland plants to fire in water limited environments. Rangelands, a Resource Under Siege. Joss PJ, Lynch PW, and Williams O B. (eds.).pp. 437-441. Cambridge University Press.

Hodgkinson, K. C. & Oxley, R. E. 1990. Influence of fire and edaphic factors on the germination of the arid zone shrubs *Acacia aneura, Cassia nemophila,* and *Donodaea viscosa.* Australian Journal of Botany. 38: 269-279.

Hopcraft, D. 1990. Wildlife land use at Athi River, Kenya. In: The improvement of tropical and subtropical rangelands. National Academy Press, Washington, D.C., pp 332-340.

Humprey, R. R. 1962. Range Ecology. Ronald Press Company, New York.

ICRA 1999. ICRA – India reports: 1999. Working document Series 78 – India. Enhancing natural resource management capacity of local communities for micro–watershed management aimed at improving sustainable production and the livelihoods of resource–poor farmers and landless people through the development of enabling technologies and biophysical indicators of their effectiveness: Analysis of three micro–watersheds in Bellary District, India. ICRA, Wageningen, The Netherlands.

Jacoby, P. W. Jr. 1986. Control and management of undesirable woody plants on semi-arid rangelands. In: Rangelands, a Resource Under Siege. Joss PJ, Lynch PW, and Williams O B. (eds.).pp. 259-262. Cambridge University Press.

Janzen, D. H. 1969. Allelopathy by myrmecophytes: The ant *Azteca* as an allelopathic agent of *Cecropia*. Ecology. 50: 146-153

Janzen, D. H. 1972. Protection of Barteria by Pachysim ants in a Nigerian rain forest. Ecology. 53: 885-892.

Janzen, D. H. 1966. Co-evolution of mutualism between ants and *Acacia* in Central America. Evolution 20: 249-275

Karban, R. & Myers, J. 1989. Induced plant responses to herbivory. Annual Review of Ecology and Systematics 20:331±348

Keesing, F. 1998. Ecology and behaviour of the pouched mouse, *Saccostomus mearnsii* in central Kenya. Journal of Mammalogy 79: 919-931.

Keesing, F. 2000. Cryptic consumers and the ecology of an African savanna. Bioscience. 50: 205-215.

Kennedy, A. D. 1998. Coppicing of *Tarconanthus camphoratus* (Compositae) as a source of sustainable Fuel-wood production: An example from Laikipia Plateau, Kenya. African Journal of Ecology. 36: 148-158.

Kingdon, J. 1997. The Kingdon guide to African mammals. Academic Press London.

Kinyamario, J. I., Trlica, M. J. & Njoka, T. J. 1995. Influence of tree shade on plant water status, gas exchange, and water use efficiency of *Panicum maximum* Jacq. and *Themeda triandra* in a Kenyan savanna. African Journal of Ecology 33: 114-123.

Kinyua, D. M. 1994: The influence of canopy cover of *Acacia etbaica* sub sp platycarpa on herbaceous production, soil moisture and fertility in Mukogodo Rangelands, Laikipia District. MSc. Thesis, University of Nairobi - Kenya.

Kironchi, G. 1992: Effects of soil type, vegetation and land use on infiltration and soil physical properties in two semi-arid catchments in Laikipia District. MSc. Thesis, University of Nairobi - Kenya.

Kriticos, D., Brown, J., Radford, I. & Nicholas M. 1999: Plant population ecology and biological control: *Acacia nilotica* as a case study. Biological Control 16: 230-239.

Kanz, W. A. 2001: Seed and seedling dynamics of certain *Acacia* species as affected by herbivory, grass competition, fire and grazing system. MSc thesis, University of Natal, Pietermaritzburg.

Lamprey, H. F. 1967. Notes on the dispersal and germination of some tree seeds through the agency of animals and birds. East African Wildlife Journal. 5: 179-180.

Lamprey, H. F. 1974. Interactions between *Acacia*, bruchid seed beetles and large herbivores. East African Wildlife Journal. 12: 81-85.

Lamprey, H. F., Halevy, G. & Makacha, S. 1974. Interactions between *Acacia*, bruchid seed beetles and large herbivores. East African Wildlife Journal. 12: 81-85.

Lamprey, H. F. 1983. IPAL woodland ecology programme: Summarised account, November 1981. In: W. Lusigi (Ed). Integrated Project on Arid Lands (IPAL) technical report Number A-5. UNESCO, Nairobi.

Lamprey, H. F. 1986. The MAB IPAL woodland ecology program in Northern Kenya. In: Joss P. J., Lynch P. W., and Williams O. B. Rangelands: A resource under siege. Proceedings of the second International Rangeland Congress. pp 349-350.

Le Houerou, H. N. (ed) 1980. Browse in Africa: The current state of knowledge. International Livestock Centre for Africa. Addis Ababa.

Le Roux, A. S. & Morris, J. W. 1977. The effects of winter burning and cutting treatments and fluctuating annual rainfall on seasonal variation in grassland basal cover. Proceedings of Grassland Society of Southern Africa. 12: 55-58.

Leuthold, W. 1996. Recovery of woody vegetation in Tsavo National Park, Kenya. 1970-1994. African Journal of Ecology 34: 101-112.

Lew, J. D. & Kammen, D. M. 1997. Review of social and environmental impacts of charcoal in Africa. Woodrow Wilson School of Public and International Affairs, Princeton University, New Jersey.

Liniger, H. P. 1992. Water and soil resource conservation and utilization on the Northwest side of Mt. Kenya. LPD-7. Berne: Group for Development and Environment (GDE), University of Berne, Switzerland.

Little, C. N. 1972. Charcoal from useless trees and shrubs. FAO Nairobi Kenya.

Lock, J. M. 1993. Vegetation change in Queen Elizabeth National Park, Uganda: 1970-1988. African Journal of Ecology 31: 106-117.

Lusigi, W. J. 1984. Integrated Resource Assessment and Management for western Marsabit District, Northern Kenya. Part 1. Integrated Project on Arid Lands (IPAL). Technical report A-6. UNESCO/FRG/MAB, Nairobi

Lusigi, W. 1983. Integrated Project on Arid Lands (IPAL). Technical Report Number A-5, UNESCO, Nairobi

Madden, D. & Young, T. P. 1992. Symbiotic ants as an alternative defence against giraffe herbivory in spinescent *Acacia drepanolobium*. Oecologia 91: 235-238

Maranga, E. K., Trlica, M. J. & Smeins, F. 1983. Water relations of *Panicum maximum* and *Digitaria macroblephara* on semi-arid rangeland in Kenya. East African Agricultural and Forestry Journal. 48: 74-80.

Mbuvi, D. & Croze, H. 1986. Utilization of Rangeland Ecosystems for wildlife conservation. In: Joss P. J., Lynch P. W., and Williams O. B. Rangelands: a resource under siege. Proceedings of the Second International Rangeland Congress pp 555-559.

McClanahan T. R. 1996. East African climate and its classification. In: McClanahan T. R. & Young T. P. (eds.). East African Ecosystems and Their Conservation. Oxford University Press, NY, pp. 244-245.

McClanahan, T. R. & Young, T. P. 1996. East African Ecosystems and Their Conservation. Oxford University Press, NY.

McNaughton, S. J. 1979. Grassland herbivore dynamics. In: Sinclair A. R. E. & Norton-Griffiths M. (eds.). Serengeti: dynamics of an ecosystem. University of Chicago Press, Chicago, pp. 46-81.

McNaughton, S. J. 1986. (5) Ecology of a grazing ecosystem: the Serengeti. Ecological Monographs. 55: 259-294.

McNaughton, S. J. & Chapin, F. S. 1985. Effects of phosphorous nutrition and defoliation on $C_4$ gramminoids on the Serengeti plains. Ecology. 66: 1617-1629.

McNaughton, S. J. & Georgiadis, N. J. 1986. Ecology of African grazing and browsing mammals. Annual Review of Ecology and Systematics. 17: 39-65.

McNaughton, S. J. & Banyikwa, F. F. 1995. Plant communities and herbivory. In: Sinclair A. R. E. & Arcese P. (eds.). Serengeti II: Dynamics, management, and conservation of an ecosystem. University of Chicago Press, Chicago, pp. 49-70.

Menault, J. C., Barbault, R., Lavelle, P. & Lepage, M. 1985. African savannas: Biological systems of humidification and mineralization. In: Tothill, J.C. and J.J. Mott (eds.). Ecology and management of the world's savanna. Australian Academy of Science, Canberra, pp. 14-33.

Midgley, J. J. & Ward, D. 1996. Tests for inducible thorn defence against herbivory must consider plant growth strategies. African Journal of Range and Forage Science. 17: 75-77.

Milewski, A. V., Young, T. P. & Madden, D. 1991. Thorns as inducible defences: Experimental evidence. Oecologia 86: 70-75.

Miller, F. M. 1994a. The costs and benefits of *Acacia* seed consumption by ungulates. Oikos 71: 181-187.

Miller, F. M. 1994b. Large herbivores, bruchid beetles and their interaction with acacia seeds. Oecologia. 97: 265-270.

Miller F. M. 1994c. The fate of mature African *Acacia* pods and seeds during their passage from the tree to the soil. Journal of Tropical Ecology. 10: 183-196.

Miller, F. M. 1995. *Acacia* seed survival, seed germination, and seedling growth following pod consumption by large herbivores and seed chewing by rodents. African Journal of Ecology. 33: 194-210.

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

Milton, S. J.1983. *Acacia tortilis* subsp. heteracantha productivity in the Tugela Dry Valley bushveld: Preliminary results. Bothalia 14: 767-772.

Milton, S. J. 1988. The effects of pruning on shoot production and basal increment of *Acacia tortilis*. South African Journal of Botany. 54: 109-117.

Milton, S. J. & Dean, W. R. J. 1995. South Africa's arid and semi-arid rangelands – Why are they changing and can they be restored? Environmental Monitoring and Assessment 37: 245-264.

Moore, E. 1974. Utilization of the habitat by the reticulated giraffe (*Giraffa camelopadalis Reticulata linnaeus*) in Northern Kenya. MSc. thesis, University of Nairobi.

Morris, C. D., Tainton, N. M., & Hardy, M. B. 1992. Plant species dynamics in the Southern Tall Grassland under grazing, resting and fire. Journal of Grassland Society of Southern Africa 9: 90-95.

Mucunguzi, P. 1995. Effects of bruchid beetles on germination and establishment of *Acacia* species. African Journal of Ecology. 33: 64-70.

Mutunga, C. N. 1995. The influence of vegetation cover on the runoff and soil loss. A study in Mukogodo, Laikipia district. MSc. Thesis, University of Nairobi.

Mwihuri, J. N. 1998. Comparative study of current vegetative status between privately and communally managed rangelands of Laikipia, Kenya. MSc. Thesis, University of Nairobi.

Myers, N. 1972. National parks in savanna Africa. Science. 78: 1255-1263.

Ndawala-Senyimba, M. S. 1972. Some aspects of the ecology of *Themeda triandra*. East African Agricultural and Forestry Journal. 38: 83-93.

NEMA (National Environment Management Authority), 2005. State of Environment report – Kenya 2004. NEMA, Nairobi, Kenya.

N'gethe, R., Njoka, T.J. & Okello, B. D. 1997. Towards a sustainable use of Mukogodo Rangelands. PRA report. Applied Research Unit and ASAL-Laikipia.

Njoka, T. J. 1990. In: Grootenhuis J. G., Njuguna S. G., & Kat P. W. 1990 (eds.). Wildlife Research for Sustainable Development. Pp 97-106. KARI, KWS & NMK.

Noble, J. C. 1986. In: Joss PJ, Lynch PW, and Williams O B. (eds.). Rangelands, a Resource Under Siege. Joss PJ, Lynch PW, and Williams O B. (eds.). pp. 557-580 Cambridge University Press

Noble, J. C., Harrington, G. N. & Hodgkinson, K. C. 1986. The ecological significance of irregular fire in Australian Rangelands. In: Joss PJ, Lynch PW, and Williams O B. (eds.). Rangelands, a Resource Under Siege. pp. 557-580 Cambridge University Press

Norton-Griffiths, M. 1979. The influence of grazing, browsing and fire on the vegetation dynamics of the Serengeti. In: Dynamics of an ecosystem. Sinclair A. R. E and Norton-Griffiths M (eds.). University of Chicago Press, Chicago.

Noy-Meir, I. 1995. Interactive effects of fire and grazing on structure and diversity of Mediterranean grasslands. Journal of Vegetation Science 6: 701-710.

Nyeki, M. D. 1993. Wildlife Conservation and Tourism in Kenya. Jacaranda Designs, Nairobi.

O’Connor, T. G. 1985. A synthesis of field experiments concerning the grass layer in the savanna regions of Southern Africa. South African National Scientific Programme Reports. 114: 1-126.

O'Connor, T. G. 1995. What role for biodiversity in the sustainable use of rangelands in developing countries? In: West, N. E. (ed). 1995. Rangelands in a sustainable biosphere. Proceedings of the Fifth International Rangeland Congress. Vol II, pp 117-120.

O’Connor, T. G. 1996. Individual, Population and Community response of woody plants to browsing in African savannas. Bulletin of the Grassland Society of Southern Africa. 7. Supplement. 14-18.

O'Connor, T. G. & Everson, T. M. 1998. Population dynamics of perennial grasses in African savanna & grassland. In: R. M Cowling, P. M. Richardson, & S. M Pierce (eds.). Population biology of grasses. V<sup>th</sup> International Range Congress Proceedings. 333-365.

O'Connor, T. G. & Crow, V. R. T. 1999. Rate and pattern of bush encroachment in Eastern Cape savanna and grassland. African Journal of Range and Forage Resources 16: 26-31

O'Connor, T. G. 2000. Community changes in rangelands – Towards improving our understanding. VI<sup>th</sup> International Rangeland Congress Proceedings Vol 1: 203-208.

Oba, G. 1990. Effects of wildfire on a semi-desert riparian woodland along the Turkwel river, Kenya, and management implications for Turkana pastoralists. Land Degradation and Rehabilitation. 2: 247-259.

Oba, G. 1994. The role of Indigenous range management knowledge for desertification control in Northern Kenya. Research report # 4. EPOS (Environmental Policy and Society) Sweden.

Oba, G. & Post, E. 1999. Browse production and off take by free ranging goats in an arid zone, Kenya. Journal of Arid Environments. 43: 183-195.

Odum, E. P. 1959. Fundamentals of Ecology. W. B. Saunders, Philadepphia and London.

Ogada, O. M. 2001. Relationships between livestock husbandry practices and depredation by carnivores in Laikipia District. M. Sc. Thesis, Kenyatta University.

Okello, B. D. 1996. Utilization of above-ground net primary production in the Mukogodo rangelands, Laikipia Kenya. MSc. Thesis, University of Nairobi.

Okello, B. D. & Young, T. P. 2001: Effects of fire, bruchid beetles and soil type on the germination and seedling establishment of *Acacia drepanolobium*. African Journal of Range and Forage Science. 17: 46-51.

Ostfeld, R. S., Pickett S. T. A. Shachak M. & Likens G. E. 1997. Defining the scientific issues in the need for a comprehensive conservation theory. In: Pickett et al. (eds.). The ecological basis of Conservation pp167-186. Chapman & Hall New York.

Outrum, D. J. 1970. Bush control with Tordon® '101' at Ol Pejeta Ranching. Twiga Chemical Industries Ltd., Nairobi, Kenya.

Owaga, M. L. 1976. Primary production and herbage utilization in Kaputei plains, Kenya. Journal of Ecology 18: 1-5.

Owen-Smith, R. N. 1982. Factors influencing the consumption of plant products by large herbivores. In: B J Huntley, B H Walker (eds.) Ecology of Tropical Savannas. Springer Verlag, Berlin.

Owen-Smith, R. N. 1983. Dispersal and the dynamics of large herbivores in enclosed areas: Implications for Management. In: Owen-Smith R. N. (ed). Management of large mammals in African conservation areas. Haum, Pretoria, pp. 127-143.

Owen-Smith, R. N. 1988. Megaherbivores. The influence of very large body size on ecology. Cambridge Studies in Ecology, Cambridge University Press, Cambridge.

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

Palmer, T. M., Young T. P., Stanton M. L. & Wenk E. 2000. Short term dynamics of an *Acacia* ant community in Laikipia, Kenya. Oecologia 123: 425-435.

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

Pickett, S. T. A. & White, P. S. (eds.). 1985. The ecology of natural disturbances and patch dynamics. Academic Press, Orlando, Florida.

Portlock, C. A., Shea, S. R., Major, A. D. & Bell, D. T. 1990. Stimulation of germination of *Acacia pulchella;* laboratory basis for forest management options. Journal of Applied Ecology. 27: 319-324.

Pratt, D. J., Greenway, P. J., & Gwynne, M. D. 1966. A classification of East African Rangelands with an appendix on terminology. Journal of Applied Ecology 3: 369-382.

Pratt, D. J. 1969. Management of arid rangeland in Kenya. British Grassland Society Journal. 24: 151-157.

Pratt, D. J. & Gwynne, M. D. 1977. Rangeland Management and Ecology in East Africa. Hodder and Stoughton, London. 310pp.

Pratt, D. J. & Knight, J. 1971. Bush control studies in drier areas of Kenya: Effects of controlled burning and grazing management on *Tarconanthus/Acacia* thicket. Journal of Applied Ecology 8: 217-237.

Prins H. H. T. 1992. The pastoral road to extinction – competition between wildlife and traditional pastoralism in East Africa. Environmental Conservation.19: 117-123.

Prins, H. H. T. & Douglas-Hamilton, I. 1989. Stability in a multi-species assemblage of large herbivores in East Africa. Oecologia (Berlin). 83: 392-400.

Prins, H. H. T. & Van der Jeugd, H. P. 1993. Herbivore population crashes and woodland structure in East Africa. Journal of Ecology. 81: 305-314.

Purdie, R. W. & Slatyer, R. D. 1976. Vegetation succession after sclerophyll woodland communities in south-eastern Australia. Australian Journal of Ecology. 1: 223-236.

Ramsey, P. M. & Oxley, E. R. B. 1996. Fire temperatures and post-fire plant community dynamics in Ecuadorian grass pàramo. Vegetatio. 124: 129-144.

Rogers, K. H. 1997. Operationalizing ecology under a new paradigm: An African Perspective. In: Pickett et al. (eds.). The ecological basis of Conservation. pp60-77. Chapman & Hall New York.

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

Roques, K. G., O'Connor, T. G. & Watkinson A. R. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. Journal of Applied Ecology. 38: 268-280.

Rosenschein, A., Tietema T. & Hall, D. O. 1999. Biomass measurements and monitoring of trees and shrubs in a semi-arid region of central Kenya. Journal of Arid Environments. 42: 97-116.

Ross, I. C., Field, C. R. & Harrington, G. N. 1976. 'The savanna ecology of Kidepo Valley National Park, Uganda: III. Animal population and park management recommendations'. East African Wildlife Journal, 14: 35-48.

Ross, J. H. 1979. A conspectus of the African *Acacia* species. Memoirs of the Botanical Surveys of South Africa. 44: 1-155.

Ruess, R. W. & Halter, F. L. 1990. The impact of large herbivores on the Seronera woodlands, Serengeti National Park, Tanzania. African Journal of Ecology. 28: 259-275.

Sabiiti, E. N. & Wein, W. R. 1987. Fire and *Acacia* seeds. A hypothesis of colonization-succession. Journal of Ecology.75: 937-966.

Sabiiti, E. N. & Wein, R. 1988. Fire behaviour and the invasion of *Acacia sieberiana* into savanna grassland openings. African Journal of Ecology. 26: 301-313.

Sabiiti, E. N., Wein, W. R. & Edroma, E. 1991. Fire and browsing: Effects on the biology of East African *Acacia* species: A review. African Wildlife Resource Management. 1: 26-29.

Salisbury, F.B. & Ross, C. W. 1985. Plant physiology. 3rd Edition. Wadsworth Publishers, Belmont, CA.

Sall, J. & Lehmi, A. 1999. JMP-IN (SAS), Start Statistics. A guide to statistics and data analysis using JMP and JMP IN software. International Thomson Publishing Company, New York.

Sandford, S. 1983. Management of pastoral development in the Third World. John Wiley and Sons Ltd., Chichester (United Kingdom).

Scanlan, J. C. & Archer, S. 1991. Simulated dynamics of succession in a North American subtropical Prosopis savanna. Journal of Vegetation Science 2: 625-643.

Scholes, R. J. & Archer, S. R. 1997. Tree grass interactions in savanna. Annual Reviews of Ecological Systems. 28: 517-544.

Seif El Din, A. & Obeid, M. 1971. Ecological studies of the vegetation of the Sudan. Journal of Applied Ecology. 8: 211-216.

Senelwa, K. & Sims, R. E. H. 1997. Tree biomass equations for short eucalypts grown in New Zealand. Biomass and Energy 13: 133-140.

Shaw, H. J. 1985. Introduction to Wildlife Management. McGraw-Hill New York.

Silvertown, J. W. & Doust, L. J. 1982. Introduction to plant population biology. Blackwell Science.

Sinclair, A. R. E. & Arcese P. (eds.). 1995. Serengeti II. Dynamics, Management, and Conservation of an Ecosystem. Chicago University Press. Chicago.

Sinclair A. R. E. & Norton-Griffiths M. 1979. Serengeti: Dynamics of an ecosystem. Chicago University Press. Chicago.

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

Smit, G. N., Rethman, N. F. G. & Moore, A. 1996. Vegetative growth, reproduction, browse production and response to tree cutting of woody plants in African savanna. African Journal of Range and Forage Science. 13: 78-88.

Smith, W., Meredith T. C. & Johns, T. 1999. Exploring methods for rapid assessment of woody vegetation in the Butemi Valley, North-central Tanzania. Biodiversity Conservation. 8: 447-470.

SNV – The Netherlands Development Organisation 2002: Analyses of target groups, institutional and governance environment in Samburu and Marsabit Districts, Kenya. Consultancy report by Bell Okello and Evelyn Njue, ETC East Africa. SNV publications, Nairobi, Kenya.

Sokal, R. R. & Rolfe, F. J. 1969. Biometry. W H Freeman & Company, New York

Stander, P. E., Nott T. B. & Mentis, M. T. 1993. Proposed burning strategy for a semi-arid African savanna. African Journal of Ecology. 31:282-289.

Stanton, M. L., Palmer T. M., Young T. P. Evans A. & Turner M. L. 1999. Sterilization and canopy modification of a swollen thorn *Acacia* tree by a plant-ant. Nature 40: 578-581.

Stapley, L. 1998. The interaction of thorns and symbiotic ants as an effective defence mechanism of swollen-thorn acacias. Oecologia 115: 401-405.

Stapley, L. 1999. Physical worker castes in colonies of an *Acacia*-ant (*Crematogaster nigriceps*) correlated with an intra-colonial division of defensive behaviour. Insect. Soc. 46: 146-149

Steel, R. G. D. & Torrie, J. H. 1980. Principles and Procedures of Statistics. A Biometric Approach. Mc Graw-Hill Book Company, New York.

Steenkamp, H. E. & Chown, S. L. 1996. Influence of dense stands of an exotic tree, *Prosopis glandulosa* Benson, on a savanna dung beetle (Coleoptera, Scarabaeinae) assemblages in Southern Africa. Biological Conservation. 78: 305-311.

Stone, G. N., Wilmer, P. & Rowe, J. A. 1998. Partitioning of pollinators during flowering in an African *Acacia* community. Ecology. 79: 2802-2827

Stuart-Hill, G. C. 1992. Effects of elephants and goats on the Kaffrarian succulent thicket of the eastern Cape, South Africa. Journal of Applied Ecology. 29: 699-710.

Swift D.M., Coughenour M. B. & Atsedu, M 1996: Arid and Semi-arid ecosystems. In: McClanahan T R and Young T P 1996 (Eds.) East African Ecosystems and their Conservation. 243-272.

Systat (SSI 1996.) Systat Software Inc. Statistical software from SSI.

Tainton, N. M., Groves, R. H. & Nash, R. 1977. Time of mowing and burning veld: Short term effects on production and tiller development. Proceedings of the Grassland Society of Southern Africa 12: 59-64.

Taiti, S. W. 1992. Vegetation of Laikipia District. Laikipia Research Program, Mt Kenya Papers, D-7. Universities of Nairobi and Bern.

Taper, M. L. & Case, T. J. 1992. Co-evolution among competitors. Oxford Survey of Evolutionary Biology. 8: 308-310.

Tchamba, M. N. 1995. The impact of elephant browsing on the vegetation in Waza N. Park, Cameroon. African Journal of Ecology. 33: 184-193.

Tchie, N. & Gakahu, G. C. 1989. Responses of important woody species of Kenya's rangeland to a prescribed burning. African Journal of Ecology. 27: 119-128.

Teague, W. R.1988a. Effects of the intensity and phenophase of defoliation and water stress on the rate of photosynthesis and recovery of carbohydrate reserves in *Acacia karroo* Hayne. Journal of Grassland of Society of Southern Africa. 5: 122-124.

Teague, W. R. 1988b. The response of *Acacia karroo* plants to defoliation by hand compared to defoliation by goats. Journal of Grassland of Society of Southern Africa. 5: 132-138.

Teague, W. R. 1988c. The response of *Acacia karroo* plants to defoliation of the upper or lower canopy. Journal of Grassland of Society of Southern Africa. 5: 225-229.

Teague, W. R. & Walker, B. H. 1988. Effect of intensity of defoliation by goats at different phenophases on leaf and shoot growth of *Acacia karroo* Hayne. Journal of Grassland of Society of Southern Africa. 5: 197-206.

Thomas, D. B. & Pratt, D. J. 1967. Bush control studies in the drier areas of Kenya. IV. Effects of controlled burning on secondary thicket in upland *Acacia* woodland. Journal of Applied Ecology. 4: 325-335

Therne, R. 1982: Study and management of large mammals. John Wiley and sons limited. New York.

Thouless, C.R. & Sakwa, J. 1995. Shocking elephants: Fences and crop raiders in Laikipia District, Kenya. Biological Conservation. 72:99-107.

Tietiema, T., Tolsma, D. J., Veenendaal, E. M. & Schroten, J. 1991. Plant responses to human activities in the tropical savanna ecosystem of Botswana. In: (Rozema J & Verkleij (eds.), Ecological Responses to Environmental Stresses. pp 262-276. Kluwer Academic Publishers, the Netherlands.

Tilley, J. M. A. & Terry, R. A. (1963). A two stage technique for in-vitro digestion of forage crops. Journal of British Grassland Society. 18: 104-111

Tothill, J. C. & Mott, J. J. (eds.) 1985. Ecology and Management of the World's savannas. Australian Academy of Sciences, Canberra.

Trollope, W. S. W. 1974. Role of fire in preventing bush encroachment in the eastern Cape. Proceedings of the Grassland Society of Southern Africa 9: 67-72.

Trollope, W. S. W. 1981. The growth of shrubs and trees and their reaction to treatment. In: Tainton N. M. (ed). Veld and Pasture management in South Africa. Shuter & Shooter, Pietermaritzburg.

Trollope, W. S. W & Trollope L. A. 2002. Fire behaviour a key factor in the fire ecology if African grasslands and savannas. Forest Fire Research & Wildland Fire Safety, Viegas (ed). Millpress, Rotterdam

Van Vegten, J. A. 1983. Thornbrush invasion in a savanna ecosystem in eastern Botswana. Vegetatio. 56: 3-7.

Verwijst, T. & Telenius, B. 1999. Biomass estimation procedures in short rotation forestry. Forest Ecology and Management. 121, 137-146.

Vesey-Fitzgerald, D. R. 1960. Grazing succession among East African game animals. Journal of Mammology 41: 161-172.

Walker, B. H. 1976. An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. Southern Africa Journal of Wildlife Research.6: 1-32

Walker, B. H., Ludwig D., Holling C. S., & Peterman R. M. 1981. Stability of Semi-arid savanna grazing systems. Journal of Ecology. 69: 473-498.

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

Wein, R. W. & Edroma, E. L. 1986. Fire in tropical Savannas with emphasis on East Africa. A biography IDRC-MR140e.

Western, D. & Gichohi, H. 1993. Segregation effects and impoverishment of savanna parks: The case for ecosystem viability analysis. African Journal of Ecology. 31: 269-281.

Western, D. & Henry, W. 1979. Economics and conservation in Third world National Parks. BioScience. 19: 414-418.

Western, D. 1989. The ecological role of elephants in Africa. *Parchyderm* 12: 42-45.

Weyerhaeuser, F. J. 1982. On the ecology of the Lake Manyara elephants. M. F. S. Thesis, Yale University.

Whelan, R. J. 1995. The Ecology of fire. Cambridge University Press.

Wyant, G. J. & Reid, R. S. 1992. Determining the age of *Acacia tortilis* with ring counts for Southern Turkana, Kenya: A preliminary assessment. African Journal of Ecology. 30: 176-180.

Young, T. P. 1984. Comparative demography of *Lobelia telekii* and *Lobelia keniensis* on Mount Kenya. Journal of Ecology. 72: 637-650.

Young, T. P. & Lindsay W. K. 1988. Role of even-age population structure in the disappearance of *Acacia xanthophloea*. African Journal of Ecology. 26: 69-72.

Young, T. P. & Francombe, C. 1991. Growth and yield estimates in natural stands of leleshwa (*Tarchonanthus camphoratus*). Forest Ecology and Management. 41: 309-321.

Young, T. P. 1987. Increased thorn length in *Acacia drepanolobium* – an induced response to browsing. Oecologia 71: 436-438.

Young, T.P., N. Patridge, & McRae A... 1995. Long-term glades in *Acacia* bushland and their edge effects in Laikipia, Kenya. Ecological Applications 5:97-108.

Young, T. P. 1996. High Montane forest and Afroalpine Ecosystems. In: McClanahan T. M., and Young T. P. (eds.). East African Ecosystems and their Conservation. Oxford University Press, New York. pp 401-424

Young. T. P., Okello, B. D., Kinyua D., & Palmer T. M. 1998. KLEE: A long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. African Journal of Range and Forage Science. 14: 94-102.

Young, T. P., Stubblefield, C. H., Isbell. L. A. 1997. Co-existence among obligate *Acacia* ants. Oecologia 109: 98-107.

Young, T. P., & Okello, B. D. 1998. Relaxation of an inducible defence: Spines in *Acacia drepanolobium*. Oecologia 115: 508-513.

# APPENDICES: TITLES OF PUBLISHED JOURNAL PAPERS AUTHORED BY BELL D. OKELLO USING DATA AND INFORMATION GATHERED DURING THE STUDY

**Appendix 1:**

Truman P. Young, **Bell Okello**, David Kinyua, Todd Palmer. 1997. KLEE: a long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. African Journal of Range and Forage Science 14:92-104 (1997).

This paper relates to chapter three and introduction to chapter four.

**Appendix 2:**

Truman P. Young and **Bell D. Okello. 1998.** Relaxation of an induced defence after exclusion of herbivores: spines on *Acacia drepanolobium.* Oecologia 115: 508 - 513(1998)

This paper relates to chapter four, specifically from section 4.5.5

**Appendix 3:**

**Okello B. D**., O'Connor T. G. and Young, T. P. 2001. Growth, biomass estimates, and charcoal production of *Acacia drepanolobium* in Laikipia, Kenya. Forest Ecology and Management 142: 143-153 (2001)

This paper was written using material from chapter seven.

**Appendix 4:**

**B. D. Okello** and T. P. Young. 2000. Effects of fire, bruchid beetles and soil type on germination and seedling establishment of *Acacia drepanolobium.* African Journal of Range and Forage Science 17: 46-51(2000).

This paper was written with material from chapter five.

**Appendix 5:**

B. D. Okello, T. P. Young, C. Riginos, D. Kelly and T. G. O'Connor 2007

Short-term survival and long-term mortality of *Acacia drepanolobium* after a controlled burn. African Journal of Ecology.

This paper was written with material from chapter five.