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THE REGENERATION ECOLOGY OF SAVANNA WOODLANDS IN RELATION TO HUMAN UTILISATION

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A thesis submitted to the Faculty of Science, University of the Witwatersrand,
Johannesburg in fulfilment of the requirements for the degree of Doctor of
Philosophy.

JOHANNESBURG

2004

DECLARATION

I declare that this thesis is my own work, unless specifically acknowledged in the text. It is being submitted for the Degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any university.

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Abstract

Little is known about the regeneration ecology of savanna woodlands. Yet this information is key to understanding woody plant population dynamics and for guiding the sustainable use of woodland resources upon which the livelihoods of many rural populations continue to depend. This study employed a combination of empirical, experimental and model formulation techniques aimed at achieving its ultimate purpose of contributing to the understanding of the regeneration ecology of savanna woody plants, particularly in relation to their utilisation by humans.

- *By contrasting woodlands under communal tenure and those in adjacent protected areas, harvesting in communal rangeland areas was found to have reduced live wood biomass and impacted on the demography of those species favoured for fuelwood. For these species, current levels of harvesting appear unsustainable, with ‘pole-size’ plants targeted, recruitment potential considerably reduced and with little evidence of compensatory recruitment.*
- Population structures showed little evidence of episodic recruitment events. Browsers or fire, by suppressing plant growth, may have a ‘smoothing’ effect that masks episodic recruitment in savanna woodlands. Interpretations of population size class distributions are additionally influenced by ‘classic’ assumptions (based on tropical forest species), e.g. of constant woody plant growth across plant size range.
- Certain savanna woody plant species appear to change their growth strategy from a ‘small plant’ phase characterised by height gain to a ‘large plant’ phase showing a reduced height relative to stem diameter increment. The height at which this shift occurs appears to coincide with the height at which woody plants are generally believed to be less vulnerable to fire damage and are considered to become reproductively mature. Yet, other species showed a relatively linear allometric relationship between height and stem diameter across sampled size range. During the sapling phase, species that showed an obvious change in growth strategy had a larger increment in height relative to stem diameter than those species characterised by a more consistent allometric relation and a higher degree of branching. Saplings of species with dense wood had a proportionally larger height gain relative to stem diameter than those with lighter wood.
- Grass cover reduced both woody plant seedling emergence and survival: both directly through competition for limited soil moisture and indirectly by influencing

seedling exposure to herbivores (particularly rodents). Field surveys documented a large cohort of seedlings that had established during a high rainfall season. Young seedlings are especially vulnerable to desiccation and damage, governing their distribution within the landscape.

- Almost all harvested plants of all species resprouted. Plant stem diameter size was the most important determinant of resprout output with both shoot number and their composite diameter increasing with increasing plant size. Cut height influenced the location of resprouting.
- A woodland model was formulated to examine spatial and temporal changes in woody plant population dynamics and wood resource availability in relation to a gradient of utilisation pressure and to alternative scenarios or harvesting strategies. Model formation proved a useful exercise for synthesising current understanding of savanna woodland systems while highlighting gaps.

The most pertinent management implications to be drawn from this study are:

- (1) Despite being vigorous resprouters, the effects of live wood harvesting are clearly evident for those species favoured as fuel wood. Other species show little human-related impact within communal rangelands and may represent a valuable alternative source of fuelwood. Harvesting of favoured species will need to be controlled to ensure future woody plant recruitment: this may include protecting sufficient reproductively mature and 'pole-size' plants to ensure future recruitment and following a rotational harvesting strategy that allows harvested plants to recover lost biomass and to become reproductive. Protecting seedlings and young plants from browsers or fire would support their rapid gain in height and harvesting value. Additional sources of fuelwood should be considered, together with alternative means of reducing the pressure on wood resources.
- (2) Resprouting biomass produced following harvesting is considerable and effectively managed could provide a valuable source of fuelwood.
- (3) The woody plants selected for this study were relatively similar in the way they responded to the environment: their seedlings required comparable conditions to become established and all were able to resprout following harvesting damage. With a few exceptions, management strategies aimed at sustainable harvesting may be able to be successfully applied across species.

Preface

This study reflects a personal interest in the ecology, conservation and politics of “cultural landscapes” in which:

- “...*the relationships between human activity and the environment have created ecological, socio-economic, and cultural patterns and feedback mechanisms that govern the presence, distribution and abundance of species assemblages*”

(Farina 2000; reference in Introduction)

- the belief that a better understanding of these systems, together with an appreciation of their conservation and economic value, are vital ingredients to ensuring the continued existence of their biodiversity and the natural resources and ecosystem services they provide to the humans who inhabit them.

DEDICATION

I dedicate this thesis to my Mom & Mike and J,

Granny & Granddad by the sea

... the octopus, pig & the kudu kudu

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My doctoral research was partly funded by the National Research Foundation (NRF) of South Africa, the University of the Witwatersrand and through collaboration with the University of Oxford's Forestry Institute by a UK/SA Science and Technology Research Fund. A stipend from the Environmental Research Centre in Leipzig, Germany, made it possible for me to spend 7 months as a Visiting Scientist in the Department for Ecological Modelling. My supervisors, Professors Norman Owen-Smith and Ed Witkowski provided me with exactly the right combination of challenges, opportunities, independence and support to nurture my growth throughout my doctoral process. I could not have had better supervisors! I would like to thank all the people that made Wits Rural Facility 'home' and a great working environment 'in the bush' for more than two years. Lorenzo Bertolo's mad sense of humour kept me 'sane'. I deeply acknowledge and give my thanks to Jazzman Zitha for his incredible assistance and companionship in the field for the duration of my research. I thank the ndunas and inhabitants of the communities in which we worked for their support and willingness to share their knowledge. David Coomes, Coert Geldenhuys, Michele Hofmeyr, Sarah Kaschula, Tim O'Connor, Joseph Ogutu, Mike Peel, Bob Scholes, Charlie Shackleton and Wayne Twine contributed their perspectives and enthusiasm for savanna ecosystems. Delali Dovie had all the answers and the bigger picture. Enormous thanks go to Frank Schurr whose statistical support and encouragement were invaluable. I have benefited tremendously from other academic links and the people who inspired me there: Nick Brown and Caroline Bampfylde of Oxford University's Forestry Institute; Juergen Groeneveld, Christian Wissel, Volker Grimm and all the people that made me feel so welcome at the UFZ in Leipzig. My gratitude for my family's support and nurturing throughout my doctoral process is infinite! I would especially like to express my appreciation to Gail Iris Neke for the generosity of her energy in formatting and editing this thesis. She, Mike Olivier, Justine Neke, Jean Nixon and Baloo were always there for me. Hernan del Valle is friend and life mentor to me. He gave me his wisdom and support to get to the other end and laughter and wonderful breaks along the way!

TABLE OF CONTENTS

Title Page	i
Declaration	ii
Abstract	iii
Preface	v
Dedication	vi
Acknowledgement.....	vii
Table of Contents	viii
Glossary	xii
List of Figures	xv
List of Tables	xvii
List of Appendices	xviii
 Chapter 1 INTRODUCTION	 1
1.1 General introduction and review.....	2
1.1.1 Savanna and the determinants of woody plant population dynamics .	2
1.1.2 Humans as modifiers of savanna.....	4
1.1.3 Woody plant seedling establishment and population recruitment	5
1.1.4 Woody plant resprouting and persistence	5
1.2 Study Region.....	6
1.2.1 Biophysical characteristics	6
1.2.2 Land use	6
1.2.3 Social and political context: socio-economic and ecological consequences.....	8
1.3 Savanna woodlands and the study species.....	9
1.4 Research rationale and objectives	10
1.5 Study approach.....	11
1.5.1 Critique of methods examining woody plant population dynamics...13	
1.5.1.1 Woody plant population dynamics and size structure analyses.....13	
1.5.1.2 Plant functional groups and syndromes of regeneration.....14	
1.5.1.3 Spatial modelling	15
1.6 Thesis structure	17
References	19
 Chapter 2 SAVANNA WOODY PLANT DEMOGRAPHY: CONTRASTING THE EFFECTS OF PROTECTION AND COMMUNAL SUBSISTENCE LAND USE ON RECRUITMENT POTENTIAL AND RESOURCE SUSTAINABILITY	 24
Abstract	25
2.1 Introduction	26
2.2 Study region	28
2.2.1 Study area and land use.....	28
2.2.2 Biophysical characteristics.....	29
2.3 Methods.....	33
2.3.1 Field data collection	33

2.3.1.1	Land use contrast.....	33
2.3.1.2	Rangeland utilisation gradient.....	34
2.3.2	Data Analysis	35
2.3.2.1	Woody plant densities and live wood biomass	35
2.3.2.2	Woody plant population structure	36
2.3.2.3	Rangeland utilisation gradient.....	38
2.4	Results	38
2.4.1	Live wood biomass and woody plant densities.....	38
2.4.2	Woody plant population structure	41
2.4.3	Rangeland utilisation gradient.....	47
2.5	Discussion	50
	References	56
Chapter 3	WOODY PLANT ALLOMETRY AND DEMOGRAPHY IN A SEMI-ARID AFRICAN SAVANNA.....	60
	Abstract	61
3.1	Introduction.....	62
3.2	Methods.....	65
3.2.1	Study area and approach	65
3.2.2	Field data collection.....	66
3.2.3	Data Analysis	66
3.2.3.1	Woody Plant Allometry	67
3.2.3.2	Population Structure and Recruitment Patterns	69
3.3	Results.....	73
3.3.1	Woody Plant Allometry	73
3.3.1.1	Population Structure and Recruitment Patterns	78
3.4	Discussion	84
	References	89
Chapter 4	ASPECTS OF THE SEEDLING NICHE: DETERMINANTS OF WOODY PLANT ESTABLISHMENT SUCCESS IN AN AFRICAN SAVANNA	92
	Abstract	94
4.1	Introduction.....	95
4.2	Methods.....	99
4.2.1	Study area and approach	99
4.2.1.1	Field factorial experiment	101
4.2.1.1.1	Grass competition or facilitation.....	103
4.2.1.1.2	Ungulate and rodent herbivory.....	103
4.2.1.1.3	Seeds and seedlings.....	103
4.2.1.2	Seedling field surveys	105
4.2.2	Statistical Analyses	107
4.2.2.1	Field factorial experiment	107
4.2.2.1.1	Seedling emergence and survival.....	107
4.2.2.1.2	Seedling size.....	108
4.2.2.2	Seedling field surveys	108
4.3	Results.....	109

4.3.1	Field factorial experiment	109
4.3.1.1	Seedling emergence and survival	109
4.3.1.2	Seedling size	113
4.3.2	Seedling field surveys	115
4.3.2.1	Land use contrast	115
4.3.2.2	Burnt and non-burnt site contrast	120
4.3.2.3	Sub-canopy and inter-canopy seedling microsites	123
4.4	Discussion	128
4.4.1	The importance of grass cover	128
4.4.2	Herbivory and its interaction with grass cover	129
4.4.3.	Seedling distribution	131
4.4.4	Seedling assemblage composition	132
4.4.5	Conclusion	133
	References	134
Chapter 5	COMPARATIVE RESPROUTING RESPONSE OF SAVANNA WOODY PLANT SPECIES FOLLOWING HARVESTING: THE VALUE OF PERSISTENCE (FOREST ECOLOGY AND MANAGEMENT, IN PRESS)	139
	Abstract	140
5.1	Introduction	141
5.2	Methods	143
5.2.1	Study area and woodlands	143
5.2.2	Field data collection	145
5.2.3	Data analysis	146
5.2.3.1	Harvester preference for woody plant species and size	146
5.2.3.2	Woody plant resprouting response	147
5.2.3.3	Resprout dieback	148
5.2.3.4	Resprout biomass and regeneration	148
5.3	Results	149
5.3.1	Harvester preference for woody plant species and size	149
5.3.2	Woody plant resprouting response	152
5.3.3	Resprout dieback	156
5.3.4	Resprout biomass and regeneration	159
5.4	Discussion	159
	References	163
Chapter 6	A MODELLED SEMI-ARID SAVANNA LANDSCAPE: DESCRIPTION OF A TOOL FOR EVALUATING STRATEGIES OF WOODY PLANT UTILISATION	167
	Abstract	168
6.1	Introduction	169
6.2	Model definition and rationale	171
6.2.1	Conceptual Definition	171
6.2.1.1	A rural settlement and its communal lands	171
6.2.1.2	A gradient of resource utilisation	172
6.2.2	Operational Definition	173

6.2.2.1	Initial woodland population and individual plant attributes	176
6.2.2.2	Rainfall.....	179
6.2.2.3	Woody plant growth.....	179
6.2.3	Wood biomass production and fuelwood demand.....	181
6.2.3.1	Woody plant harvesting	181
6.2.3.2	Stump recovery	184
6.2.3.3	Woody plant ageing, mortality and deadwood production	184
6.2.3.4	Seedling dispersal.....	186
6.2.3.5	Seedling establishment.....	188
6.3	Gaps in understanding and knowledge of savanna woody plants...	188
6.3.1	Expected model outcomes.....	189
6.4	Concluding comment	190
	References	191
Chapter 7	SYNTHESIS AND GENERAL DISCUSSION.	193
	The regeneration ecology of savanna woody plants in relation to human utilisation.....	194
7.1	Introduction.....	194
7.1.1	Recovery following disturbance: ‘natural’ versus human-related disturbances.....	194
7.2	Integration of ecological findings and additional insights	196
7.2.1	Savanna woody plant population structure in relation to human utilisation.....	196
7.2.2	Woody plant regeneration.....	197
7.2.2.1	Seedling establishment.....	198
7.2.2.2	Resprouting ability	199
7.2.3	Woody plant response groups	199
7.3	Management implications and recommendations.....	200
7.4	Woodland model synthesis and the gaps in understanding.....	202
7.5	Sustainable savanna woodland management	203
	References	206
	APPENDICES	208

GLOSSARY OF FREQUENTLY USED ECOLOGICAL TERMS

(references in Introduction)

Allometry: the study of the change in proportion of various parts of an organism as a consequence of growth.

Browsers: defined as ungulates with a diet composed of more than 75% leaf matter (Mendoza *et al.* 2002).

Bushes: Long-lived woody plants shorter than trees but taller than 1 m. They have escaped grass competition but remain vulnerable to fire and browsing. Bushes and shrubs are frequently multi-stemmed from or near the base (Lawes *et al.* 2004).

Degradation: loss of economic potential to produce goods/services of direct human-use value; loss of ecological function necessary to maintain ecosystem processes; loss of biodiversity at ecosystem, community or genetic level. In relation to rangelands: replacement of high quality fodder perennial grasses by unpalatable perennials and annuals, soil erosion and an increasing density of woody plants.

Disturbance: broadly defined as any discrete event in time that disrupts ecological processes and/or structures (ecosystem, community, or population) by influencing resource availability or changing the physical environment (White & Pickett 1985) (the terms, *Pressure* or *Stress*, imply a longer-term more continuous influence or impact).

Grazers: defined as ungulates with a diet composed of more than 75% grass biomass (Mendoza *et al.* 2002).

Microsite: refers here to the immediate environment within which a woody plant seedling is growing. Characterised by properties including light incidence, soil type, available moisture, nutrients and surrounding plants.

Plant functional group: a non-phylogenetic classification leading to a grouping of organisms with similar traits that respond in a similar way to a syndrome of environmental factors (Gitay & Noble 1997).

Recruitment: the addition of new individuals into a population, following the young plant to adult (reproductively mature) transition. The key constraint on recruitment involves escaping the herbaceous layer, where woody plants are vulnerable to competition from grasses and damage by fire and herbivores.

Regeneration: population recruitment arising from seeds and seedling establishment or vegetative growth. The major mode of occupation of new space is by seedlings, however, certain woody plant species have the capacity to regenerate

from root suckers especially when aboveground parts are damaged. Many savanna woody species are able to persist following damage, recovering lost biomass through resprouting.

Advanced regeneration: regeneration by established seedlings and saplings (i.e. from sapling bank) resulting in strong recruitment in response to a release from suppressing factors (see **Storage effect**).

Resprouting: The terms *coppicing/resprouting/sprouting* have been used interchangeably in the literature. For the purposes of this study, *resprouting* is used to denote shoots growing from the stem or stem base/root crown of a plant following damage e.g. from harvesting.

Root suckers: resprout shoots originating from the roots of a plant that may become independent of the parent plant - representing an alternative mode of regeneration.

Sapling: a juvenile plant, structurally simple but having progressed beyond the seedling stage. They no longer have cotyledons; often have mature forms of leaves, shoots and roots.

Savanna: The largest biome in southern Africa, accounting for 45% of southern African vegetation and 35% of the vegetation of South Africa. The major environmental delimiting factor is limited rainfall that prevents the woody component from dominating, while the effects of fire and grazing maintain grass layer presence (Scholes & Walker 1993, Van Rooyen & Bredenkamp 1996).

Semi-arid savanna: mean annual rainfall is less than 750 mm per annum. The primary determinant of plant growth is moisture, with rainfall characterised by high spatial variability within seasons, high variability between years and recurrent but unpredictable droughts. Rising mean annual temperatures in many regions are causing increasing aridity.

Seedling: defined here as a young woody plant, less than 0.5 m in height and smaller than 1 cm in stem diameter, with a supple non-woody stem and frequently bearing cotyledons.

Seedling establishment: young seedlings have sufficiently expanded a photosynthetic surface, extended their root system and accumulated belowground resources, thus having a higher probability of surviving adverse conditions.

Shrubs: Woody plants shorter than 1 m, competing directly with grasses for light and space (Lawes *et al.* 2004).

Size class distribution: a graphical representation of population structure: in this case of the number of woody plants represented by stem diameter size categories of equivalent intervals.

Storage effect: During years with conditions favourable for seedling regeneration, a species can establish a cohort of juveniles and once established these individuals are able to persist in adverse conditions. Reproductive potential is thus “stored” between generations, allowing the population to recruit strongly when conditions are favourable (Chesson & Warner 1981).

Sustainable harvesting: (forest) harvesting methods are generally designed to ensure that the harvest interval allows the ecosystem to recover from the last harvest (an ecological rotation). A sustained yield is defined as a non-declining, continual supply of wood over decades or centuries, or at least over multiple rotations. However, ecologically sustainable yields seldom meet socio-economic needs and no harvest strategy is likely to be sustainable without some management of users. Balancing the short-term subsistence needs of rural people with the long-term requirements of future generations is a significant challenge.

Sustainable natural resource utilisation: defined as the wise use of present resources without compromising the ability of future generations to meet their resource demands (WCED 1987).

Trees: Plants with a normal lifespan greater than 10 years, which can grow to at least 2.5 m height with adequate water, lights and nutrients and if not browsed, cut or burned; in which more than four fifths of the aboveground dry biomass consists of wood by the time reaches two thirds of its potential height (Lawes *et al.* 2004).

Woodlands: Vegetation formations dominated by trees, but not to the extent that other growth forms are excluded or restricted to minor niches. Although woodlands are the woody end of the savanna spectrum, they contain a significant grass component and tree canopies are not continuous or overlapping (Scholes & Walker 1993, Van Rooyen & Bredenkamp 1996).

Broad-leafed woodlands: In contrast to fine-leafed woodlands, occur on infertile soils in higher rainfall areas, at higher altitudes and cooler temperatures. Associated with granitic, sandstone and sandy substrates (derived from Africa erosion surface). Less productive grazing resources relative to fine-leafed woodlands.

Woody plants: collective term for trees and shrubs (Lawes *et al.* 2004).

LIST OF FIGURES

Chapter 1

Figure 1. Simplified model of savanna dynamics.	3
Figure 2. Map of the study region.	7
Figure 3. Study structure.	17

Chapter 2

Figure 1. Map of the study region.	30
Figure 2. Density of woody plant species in communal rangelands and protected areas.	39
Figure 3. Stem diameter distributions of study species in communal rangelands and protected areas.	42
Figure 4. Mean stem number per woody plant in communal rangelands and protected areas.	48
Figure 5. Stem diameter distributions for woody plant species with distance from Thorndale settlement.	51

Chapter 3

Figure 1. An example of a plot of deviances.	68
Figure 2. Relationship between woody plant height and basal stem diameter for each of the study species.	75-76
Figure 3. Predicted relationships between woody plant height and stem diameter for saplings of the study species.	77
Figure 4. Stem diameter distributions for the study species within protected areas and adjacent communal rangelands.	79-80
Figure 5. Woody plant height distribution of <i>Sclerocarya birrea</i>	81
Figure 6. Quotients plots of woody plant frequencies in successive size classes.	83

Chapter 4

Figure 1. Map of the study region.	100
Figure 2. The factorial experiment designed to assess the influence of herbaceous cover and herbivory on woody plant seedling establishment.	102
Figure 3. The number of emergent and surviving <i>Strychnos madagascariensis</i> seedlings in relation to plot treatment.	113
Figure 4. Stem diameter distributions of seedlings in the field.	118
Figure 5. Stem diameter distributions of seedlings sampled in protected areas and communal rangelands.	119
Figure 6. Stem diameter distributions of seedlings in a recently burnt site and in a non-burnt site.	122
Figure 7. Stem diameter distributions of seedlings growing beneath the canopies of other woody plants and those growing in inter-canopy areas.	127

Chapter 5

Figure 1. Relative density of woody plant species and the proportion of stems harvested.	150
Figure 2. Stem diameter distributions of woody plant species and the proportion of each size class harvested.	151
Figure 3. Resprout shoot number in relation to plant size.	155
Figure 4. Composite resprout shoot diameter in relation to plant size.	157
Figure 5. 'Resprouting vigour' in relation to plant size.	158

Chapter 6

Figure 1. Conceptual diagram of the determinants of woody plant growth and demography.	174
Figure 2. Diagram of the disturbance gradient and modelled transect outward from a settlement.	175
Figure 3. Diagram of the variables influencing of woody plant growth.	180
Figure 4. Diagram of the modelled live wood harvesting process.	183
Figure 5. Diagram of the modelled process of woody plant mortality and ageing.	185
Figure 6. Diagram of the modelled process of seed dispersal and establishment.	187

LIST OF TABLES

Chapter 2

Table 1. Woody plant densities in communal rangelands and protected areas, with the species composition of cut woody plants.....	40
Table 2. Kolmogorov-Smirnov test results of statistical difference in population size class distributions.....	45
Table 3. Comparison of woody plant parameters within communal rangelands, along a utilisation gradient with distance from Thorndale settlement.	49

Chapter 3

Table 1. Details of the study species, including description of growth form and wood density.	70
Table 2. Regression equations of the relationship between stem diameter and height for each of the study species.	74
Table 3. Measures of population size structure of the study species within protected areas and communal rangelands.	82

Chapter 4

Table 1. The proportion of seedlings emerging and surviving after each season under each grass treatment.	110
Table 2. Generalised linear model analysis of <i>Strychnos madagascariensis</i> seedling emergence and survival in response to grass treatment and protection from herbivory.	112
Table 3. Generalised linear model analysis of the influence of grass treatment and protection from herbivory on <i>Strychnos madagascariensis</i> seedling size.	114
Table 4. Size of <i>Strychnos madagascariensis</i> seedlings that survived at the end of the first growing season, through the dry winter period and those that did not.	115
Table 5: Number of seedlings sampled within protected areas and communal rangelands, contrasted with densities of reproductively 'mature' woody plants for the same sites.	117
Table 6. Seedling size contrasted for protected areas and communal rangelands.	120
Table 7. <i>Sclerocarya birrea</i> seedling size contrasted between a burnt and non-burnt site.....	123
Table 8. The number of seedlings per woody species occurring beneath canopies and in inter-canopy areas.	124
Table 9. Distance of seedlings from the nearest potential 'parent' plant.....	124
Table 10. Seedling size and leaflet number contrasted for seedlings growing beneath canopies and in inter-canopy areas.....	126

Table 11. Generalised linear model analysis of the association of seedlings (by species and size) with sub- and inter-canopy microsites.	129
---	-----

Chapter 5

Table 1. Regression equations of best-fit generalised linear models for the most influential factors determining woody plant resprouting response.	153
---	-----

Table 1 (cont). Significance testing of best-fit generalised linear models for the most influential factors determining woody plant resprouting response.	154
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LIST OF APPENDICES

APPENDIX 1. Patterns in woody plant populations in relation to human use in a South African Savanna (Paper presented by Kirsten S. Neke at the Natural Forests and Savanna Woodlands Symposium III, 2002. Kruger National Park, South Africa)	209
APPENDIX 2. Nomenclature of the study species and general description of their growth form..	226
APPENDIX 3. Herbaceous cover along a gradient of rangeland utilisation intensity.	227
APPENDIX 4. Influence of land use on the allometric relationship between woody plant height and stem diameter.....	229
APPENDIX 5. Woody plant population structure: further descriptive functions.	230
APPENDIX 6. Woody plant height distribution within protected areas and communal rangelands.....	234
APPENDIX 7. Species composition of the harvested study site.	235
APPENDIX 8. Resprouting response of the dominant woody plant species.....	236
APPENDIX 9. Calculation of pre- and post-harvest wood biomass for the study site.	237
APPENDIX 10. Assumptions made in developing the woodland model.	238
APPENDIX 11. Observations of woody plant dynamics by resident resource users.....	241

CHAPTER 1

Introduction

1.1 GENERAL INTRODUCTION AND REVIEW

1.1.1 Savanna and the determinants of woody plant population dynamics

Savannas cover approximately one half of the land surface of Africa, making them the most extensive African biome and the largest in southern Africa (Scholes & Walker 1993, Van Rooyen & Bredenkamp 1996). Globally, savannas cover a large area of the tropics, are inhabited by a fifth of the human population and support the majority of the world's livestock and large mammals (Scholes 1997). Their importance lies in the large contribution they make to informal and subsistence economies through the supply of grazing, fuelwood, timber and other resources, their contribution to the formal economy as the main location of the livestock and ecotourism industries, their global impact through the emissions of trace gases from fires, soils, vegetation and animals, the sequestration of carbon and their biological diversity. Savanna areas are both increasing due to deforestation and abandoned agriculture and decreasing due to cultivation and degradation, although the balance is probably a decrease, which is likely to be accentuated in the foreseeable future under population pressure and land use changes.

Savannas are highly dynamic systems, alternating in the relative dominance of their herbaceous and woody components according to soil properties, prevailing rainfall, herbivory and human activity (Figure 1 on page 3). Rainfall and soil nutrients are considered the key determinants of savanna woody plant composition and demography. They determine the influence of fire and herbivory which act as 'modifiers' of the savanna state (Huntley & Walker 1982, Scholes *et al.* 1997, Sankaran *et al.* 2004). The relative influence of each factor on woody plant demography, operating separately or interactively, differs in relationship to environmental context and in human-modified landscapes, with land use. It also differs according to the woody species and plant life history stage affected, the levels of damage inflicted, the period over which the impact is sustained and the season in which it occurs.

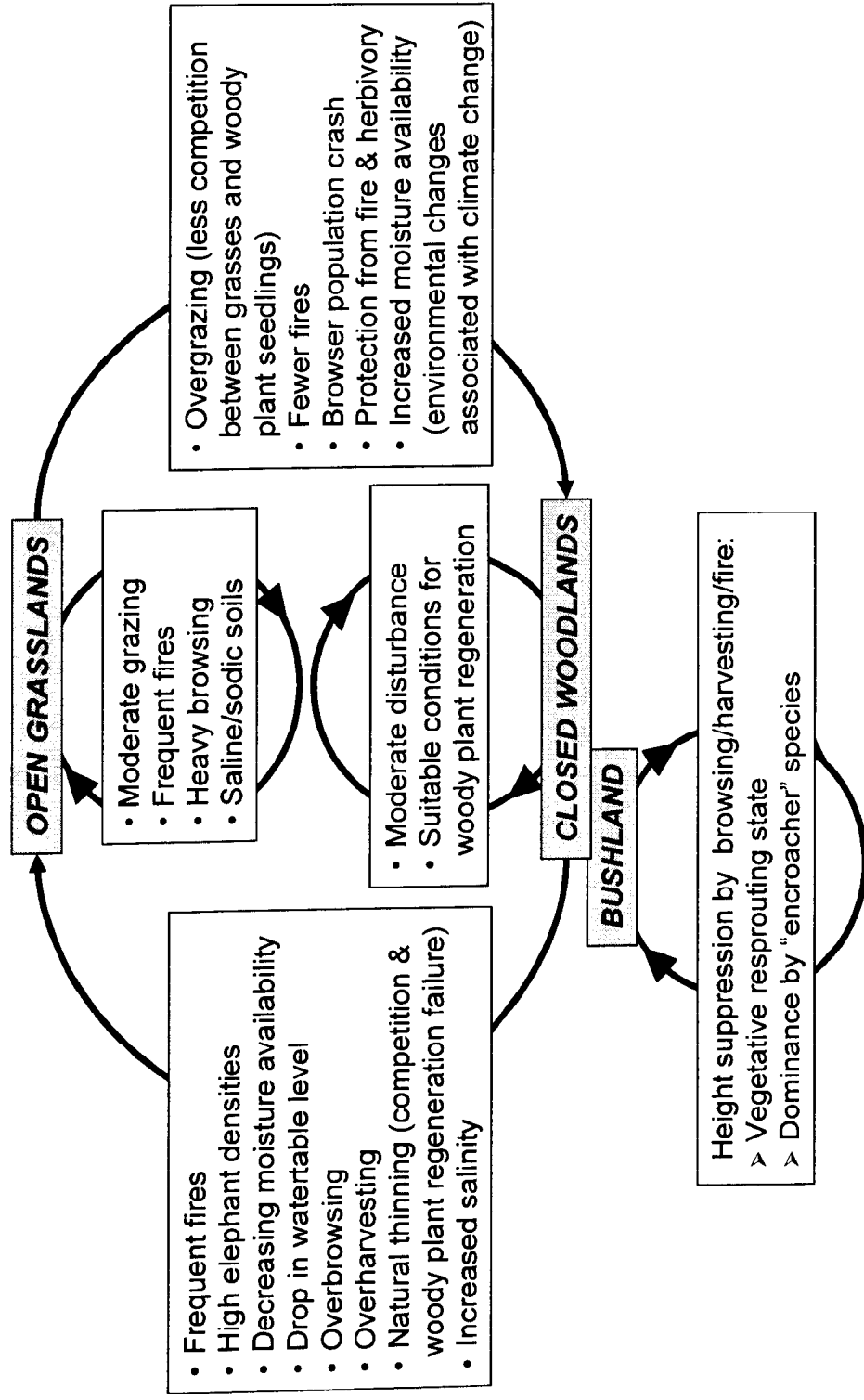


Figure 1. Simplified model of savanna dynamics and the primary determinants of the relative dominance of herbaceous and woody plant components (adapted from Belsky 1989).

1.1.2 Humans as modifiers of savanna

Human use of savanna woodlands is not a recent phenomenon in Africa. Harvesting, livestock grazing/browsing and human-ignited fires, extending back to agro-pastoralist iron-age peoples, were a significant part of the disturbance regime that led to the woodland structure and composition observed early in the colonial period (Scholes 1997). Even in relatively 'undisturbed savannas', humans have indirectly influenced vegetation by altering fire regimes and the suite of browsers present. Megaherbivores, and especially elephants, can radically alter savanna vegetation over large areas, damaging mature woody plants and influencing seed production, suppressing the growth of small plants and their recruitment (Owen-Smith 1988, Barnes 2002). Under extreme conditions where elephants are crowded into small areas, they can transform wooded savanna into open grassy savanna (Prins & Van der Jeugd 1993).

Human impact in savanna environments frequently leads to vegetation changes that are more rapid and extensive than natural transformations. It can be highly species- and size-selective, often taking the form of continuous and widespread pressures, through sustained grazing, frequent fires, wood harvesting and clearing for agriculture and settlement (Lykke 1998). Increases or decreases in the frequency or intensity of these practices can lead to extensive changes in woodlands (Hoffman 1996). A thickening of woodlands has frequently been documented following overgrazing of the savanna grass layer and a subsequent reduction in fire frequency (Skarpe 1990, 1991, Tainton 1999). Grazing reduces grass biomass, enabling seedlings to establish and allowing already established seedlings and saplings to escape fire suppression (Witkowski & Garner 2000). In overgrazed systems, fire has less of an influence on woody plant recruitment than browsers. Browsers, in a similar way to fire, may limit growth and prevent woody plants from attaining reproductive maturity (Bond & Midgley 2001). A decrease in browsing pressure or a suppression of grass growth through grazing or drought, may allow suppressed woody plants to attain vertical dominance, lowering their vulnerability to subsequent damage (Prins & Van der Jeugd 1993, Scholes & Archer 1997).

1.1.3 Woody plant seedling establishment and population recruitment

For woody plants with long life spans and little post-establishment mortality, establishment limitation is likely to be one of the strongest filters on woody plant recruitment (Harper 1977, Clark *et al.* 1998). Savanna woody plants are especially vulnerable as young seedlings - to dry periods during the wet season, to competition with grass for limited soil water and nutrients, to fire, and herbivory by mammals and insects (O'Connor 1995, Scholes & Archer 1997, Wilson & Witkowski 1998, Higgins *et al.* 2000). Knowledge is poor as to the relative importance of these factors in limiting seedling establishment. For plant population dynamics in arid and semi-arid regions, temporal variation in rainfall and soil moisture availability is of particular importance and it is likely that wet-season droughts strongly influence seedling establishment patterns (Wiegand *et al.* 1995, Higgins *et al.* 2000). Seedling establishment may in many contexts be a rare occurrence, requiring the coincidence of sufficient rainfall and protection from damage. Recruitment into the mature plant population similarly requires favourable growing conditions, including a release from browsing and fire pressures. Many species may have a large proportion of their population suspended in a stunted condition within the grass layer (Silvertown & Doust 1993). Such a "seedling bank" may allow rapid recruitment when conditions are appropriate - the so-called "storage effect" (Chesson & Warner 1981).

1.1.4 Woody plant resprouting and persistence

Many savanna woody plant species are able to survive damage, recovering lost biomass through resprouting. Until recently, the importance of resprouting was neglected, with research on plant regeneration focusing on seeds and seedlings, with the implied importance of replacement rather than persistence (Bellingham & Sparrow 2000, Bond & Midgley 2001). In some species, resprout shoots (or root suckers) originating from the roots of a plant, may give rise to independent plants by an alternative vegetative mode of regeneration. Woody plants differ in their resprouting ability. The emerging generalisation is that woody plant species that resprout vigorously as adults tend to be poor recruiters, whereas non-resprouters recruit more readily. There appears to therefore be a trade-off between resprouting to

rebuild biomass and producing seed to re-occupy the same or more distant sites in the future (Kruger *et al.* 1997, Bond & Midgley 2001).

1.2 STUDY REGION

1.2.1 Biophysical characteristics

The research upon which this thesis is based took place within the Bushbuckridge district, in the southernmost section of South Africa's Limpopo Province (centering on 31° 17' E; 24° 39' S). The study region spanned the area east of Acornhoek (the largest settlement in the region) to the Manyeleti Reserve, bordering the Kruger National Park (Figure 2 on page 7). The region is characterised by low rainfall (ca. 650 mm per annum in the west; ca. 550 mm per annum in the east), concentrated in the summer season (October to May). This is mainly in the form of convectional thundershowers (Shackleton 1997). Intra-seasonal drought is common with more prolonged drought occurring as often as every 3.5 years. Mean annual temperature is 22° C. Mean daily maxima are approximately 30° C in January and 23° C in July. The topography of the study region is gently undulating. Soils are underlain by granitic gneiss with local intrusions of gabbro.

1.2.2 Land use

The term 'communal rangelands' refers to the vegetated land under communal tenure surrounding rural (in some cases peri-urban) settlements. The main uses of this land are for livestock grazing and the harvesting of natural resources (Pollard *et al.* 1999). Densities of indigenous herbivores within communal rangelands are negligible. Livestock (cattle and goats) grazing has reduced grass biomass surrounding settlements and subsequently the intensity and extent of fires. Following land under communal tenure, the second largest use of land within the Bushbuckridge region is for protected areas. Protected areas are state- or privately-owned game reserves used for wildlife conservation, ecotourism and hunting. These differ in the time since proclamation and in their management of indigenous mammal numbers and fire regimes. Grazing pressure is relatively lower than in communal rangelands with high densities of livestock. Protected areas are fenced

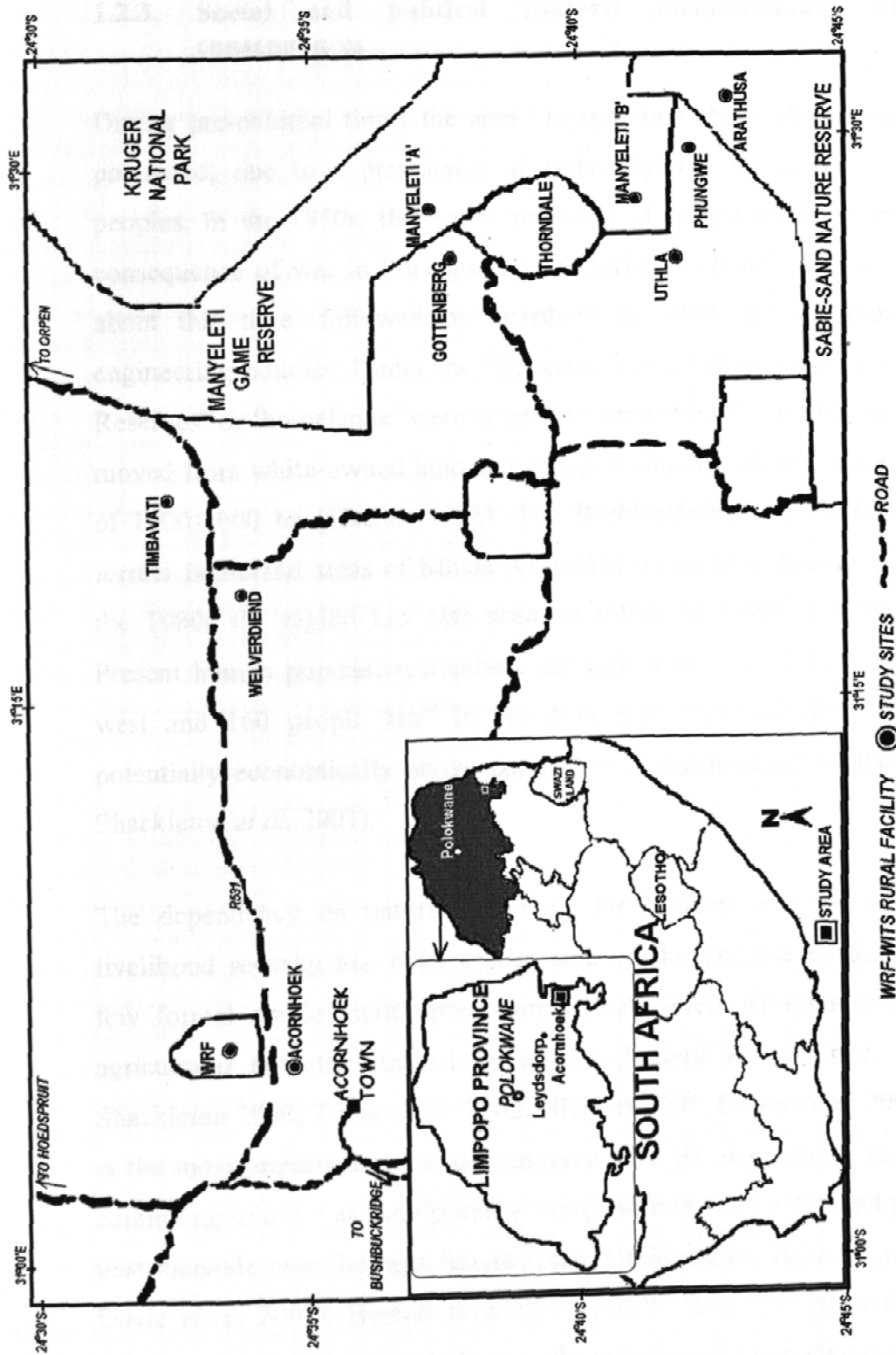


Figure 2. Map of the Bushbuckridge study region, Limpopo Province, South Africa. Paired study sites in communal rangelands and protected areas are indicated. Additional sampling was carried out in the woodlands surrounding Thorndale. (D. Dovie is thanked for his help in map creation).

and there has been limited harvesting of woodland resources with neighbouring communities largely denied access.

1.2.3 Social and political context: socio-economic and ecological consequences

During pre-colonial times the area incorporating the study region was sparsely populated, due to a prevalence of tsetse fly and malaria, by sotho-speaking peoples. In the 1850s, there was an influx of tsonga-speaking immigrants as a consequence of war in Portuguese East Africa. Colonial penetration occurred at about this time, followed by apartheid in 1948 and its supporting social-engineering policies. Under the “Betterment and Villagisation” policies, ‘African Reserves’ or ‘homelands’ were created to control land, with blacks being forcibly moved from white-owned land and grouped into centralised settlements on farms of 1000-2000 ha (Fischer 1996). The Bushbuckridge region forms part of the former homeland areas of Mhala (Gazankulu) and Mapulaneng (Lebowa). Since the 1980s the region has also seen an influx of refugees from Mozambique. Present human population numbers are high: more than 300 people km⁻² in the west and 160 people km⁻² in the drier east. Approximately 60-70% of the potentially economically active population is unemployed (Pollard *et al.* 1999, Shackleton *et al.* 2001).

The dependency on natural resources for survival and for some degree of livelihood security has been exacerbated by the underdeveloped infrastructure, few formal employment opportunities, high levels of migrant labour and an agricultural potential limited by aridity (Pollard *et al.* 1999, Shackleton & Shackleton 2000, Twine *et al.* 2002, Niehaus 2001, Dovie *et al.* 2002). Fuelwood is the most important woodland resource with the majority of rural households continuing to use it as their primary energy source, with a demand predicted to be unsustainable over the next few decades (Griffin *et al.* 1992, Banks *et al.* 1996, Dovie *et al.* 2002). Human population growth rates are high and there is little hope of poverty alleviation or large-scale adoption of alternative energy sources in the near future.

The effect of human disturbance within the study area is conspicuous. There is a distinct change in species composition and vegetation structure with distance from settlements, suggesting that vegetation patterns within communal areas are related to levels of resource harvesting and grazing pressures (Shackleton *et al.* 1994, White 1999). High levels of human disturbance have been found to result in a decrease in woody biomass, species richness and woody plant density, together with changes in vegetation structure including a decrease in height classes and basal stem area. In a comparison of woody plant community composition and population structure in communal grazing lands, commercial cattle farms and protected areas, communal grazing lands had fewer small and large individuals suggesting both lower levels of regeneration and regenerative capacity (Higgins *et al.* 1999).

The cultural, economic and political transitional phase in which rural societies in the Bushbuckridge district are at present, is associated with a breakdown of the local, traditional, informal and formal set of rules controlling land and resource utilization. The dysfunction of common property governance into open access and the increase in external users harvesting resources in the settlements are major sources of concern and are important in driving landscape change in the area. There is an absence of alternative local resource-management institutions, of fundamental importance for the sustainability of rural communal systems (Shackleton *et al.* 2001, Twine 2002). As a consequence, communal lands become increasingly vulnerable to resource exploitation for commercial gain. Such disintegration of community management structures and the consequent degradation of woody plant resources have been reported from other community-controlled forests and woodlands in southern Africa (Grossman & Gandar 1989, Shackleton 1993, Vermeulen 1996, Geldenhuys 1997).

1.3 SAVANNA WOODLANDS AND THE STUDY SPECIES

The savannas of South and East Africa can be broadly divided into two types: those growing on nutrient-rich substrates, mostly in low-lying areas, and those growing on the well-drained nutrient-poor substrates of upland areas. Nutrient-

rich savannas are dominated by the ‘fine-leaved’, thorn-bearing Mimosaceae. They support a higher grass production, greater densities of herbivores and have been more extensively researched than nutrient-poor savannas. Nutrient-poor savannas, upon which this study focuses, are characterised by a virtual absence of thorns and leaves several centimetres in diameter (Scholes & Walker 1993). Members of the Combretaceae and Caesalpiniaceae dominate these ‘broad-leaved’ savanna woodlands.

Vegetation of the study region is broadly classified as Mixed Lowveld Bushveld and is dominated by species of the Combretaceae (Van Rooyen & Bredenkamp 1996). The Combretaceae, represented by 19 genera and 600 species, are cosmopolitan in the tropics and subtropics, and are well-represented in South Africa as trees and shrubs. *Combretum*, the largest genus, has entire, opposite leaves without stipules. Fruits are characteristically 4-5 winged and single-seeded. Members of the second largest genus *Terminalia* often have a distinctive pagoda-like tree architecture, the main stem producing whorls of horizontal lateral branches, each with the tip turned up and a cluster of leaves at its apex. Combretaceae flowers are usually inconspicuous, small, greenish or yellowish-white, and clustered in axillary heads or spikes. The fruit of *Terminalia* and most other members of the Combretaceae is surrounded by a single wing (Coates Palgrave 1977, Van Wyk & Van Wyk 1997). *Terminalia sericea* is one of the most widespread woodland species in southern Africa (Shackleton 2001). It typically occurs on deep sandy soils in association with other species but may form monospecific stands along seep lines or following disturbance. Shallower or rocky, infertile soils are dominated by *Combretum apiculatum* in semi-arid areas giving way to *C. collinum* in slightly wetter parts. Most Combretaceae are important sources of fuelwood. Additionally, the marula *Sclerocarya birrea* and sickle bush *Dichrostachys cinerea* contribute considerably to the woody biomass of the study region (Shackleton 1997).

1.4 RESEARCH RATIONALE AND OBJECTIVES

Savanna ecosystems and dynamics are currently poorly understood with less attention given to these areas in the past compared to tropical forests or temperate grasslands. Research has been biased towards studies on large mammals, tree-grass interactions, fire and production ecology. The pressures of human use will focus research on production ecology in the coming decades, but an increasing emphasis on conservation, rehabilitation and possible climate change will require a more detailed understanding of processes at the organism level, including reproductive biology and life-history characteristics (Scholes 1997). An improved understanding of savanna woodland regeneration processes is important for managing these highly dynamic and heterogeneous ecosystems and in predicting trends in population dynamics (Higgins *et al.* 2000, Witkowski & Garner 2000, Wilson 2002). This study investigated the regeneration ecology of several savanna woody plant species. As described above, the study was carried out within a region in South Africa where rural populations continue to depend on natural resources (particularly fuelwood) for livelihood and subsistence needs. A similar situation exists throughout much of Africa, with resource harvesting acting as a “safety net” that allows households to survive in semi-arid savanna areas of poor agricultural potential and with few formal employment opportunities (Shackleton & Shackleton 2000). Ultimately, through contributing to our understanding of woody plant regeneration, this study aimed to be of value in guiding the conservation and sustainable utilisation of savanna woodlands.

The specific objectives of the study were to:

- Document and contrast the densities and population structures of several savanna woody plant species in relationship to land use and associated disturbances/influential factors.
- Evaluate whether woody plant species differ in their growth and regeneration strategies.
- Investigate the determinants of seedling establishment success.
- Establish the relative resprouting response of savanna woody plants following harvesting.

- Formulate a woodland model that supports an investigation of the spatio-temporal dynamics and regeneration of woody plant populations, in relationship to their utilisation by humans.

1.5 STUDY APPROACH

Gaining an understanding of the population dynamics and regeneration of savanna woody plant species is problematical for several reasons: savanna woody plants are long-lived, difficult to age and reveal irregular population dynamics (including growth and recruitment) in response to erratic and only episodically favourable environmental conditions. To document the regeneration ecology of savanna woody plant species ‘in real time’ would therefore require a study duration spanning well beyond that of an average field or Ph.D. study. This study, therefore, assumed the approach of an ‘ecological detective’, employing a combination of empirical, experimental and model formulation techniques to accomplish its objectives.

Savanna woody plant population dynamics and land use: Within the study region, the close proximity of several settlements to protected areas facilitated a comparison of the woodlands of communal rangelands with those of adjacent protected areas. Woody plant population structure was contrasted using size class distribution analyses (further discussion of the use and interpretation of size class distributions follows below).

Study species represented a range of woody plant characteristics: Several woody plants species were selected as study species, differing from one another in features including plant growth form, wood density, leaf size, mode of seed dispersal and apparent desirability to humans (for fuelwood) or herbivores (for browse). Together they represented the majority of the species most common within both communal rangeland and protected areas of the study region.

Seedling establishment: “Little is known about the regeneration niches of savanna woody plants” (Higgins *et al.* 2000). There are few studies that have focused on small seedlings, as it requires intensive fieldwork to thoroughly search for them.

Most of these do not distinguish true seedlings from resprouts/root suckers (Wilson & Witkowski 2003). This study used a combination of intensive field observations of seedlings (documenting the characteristics of the microsites in which they grew) and an experimental study to assess the determinants of seedling establishment success. The experiment examined the influence of grass competition (or facilitation) and herbivory on seedling emergence and survival. Drought and fire are known to be overriding factors resulting in mortality of young seedlings of all species. The study did not explicitly examine these factors. In carrying out the experimental study, supplementary water during the vulnerable seedling pre-establishment stage limited desiccation. Evidence of fire (and other) damage to seedlings located during field surveys was documented.

Woody plant resprouting vigour: Resprouting response is difficult to quantify as there is a continuum of responses to disturbances of varying severity, with species often diverging in their resprouting response at different life history stages (Bond & Midgley 2001). The relative resprouting capacity of woody plants of different species and size was documented following the intensive harvesting of a previously protected area over a short time period.

Woody plant 'architecture' and growth strategies: Woody plant allometry (the relationship between height and stem diameter) and species-specific characteristics (wood density, extent of stem branching and maximum height attained) were contrasted to determine whether species showed different growth strategies in response to their environments.

Woody plant functional/response groups: Classifying species into functional or response groups (e.g. species that are similar in their dominant mode of regeneration or growth strategy) enables generalisations to be drawn in relation to their response to particular factors. Such simplification is valuable for ecological modelling. The study's empirical findings were used to deduce the value of functional/response group classification, acknowledging that a larger number of species is needed for this classification to be more rigorous (plant functional classification is reviewed below).

Predicting long-term spatial woody plant population dynamics: Simulation modelling can be a powerful tool for gaining insights into the ‘bigger picture’: supporting an exploration and prediction of population dynamics over longer time periods and larger spatial scales. A woodland model was formulated to assess the relative importance of variables in determining woody plant population dynamics and the consequences of alternative scenarios or harvesting strategies (the use of spatial modelling is discussed further below).

Resource user knowledge of woody plant population dynamics and regeneration: Resource users were interviewed about the resource base. Questions and discussions explored issues including: observed vegetation changes including species increasing or decreasing in density, woody species that are most highly appreciated for fuelwood and other uses, the main causes of declines, regenerative potential (seedlings and resprouting) of different savanna woody plant species, and proposals for natural resource management. Participatory Rural Appraisal (PRA) methods were used, including mapping, quantifying, ranking and group discussions.

1.5.1 Critique of methods examining woody plant population dynamics

1.5.1.1 Woody plant population dynamics and size structure analyses

It takes many years of field research to gain an understanding of the population dynamics of long-lived woody plants and present ecological knowledge is rather poor. Size class distributions have been used to gain rapid insights into the long-term dynamics of woody plants, with a population’s size structure considered the outcome of past demographic events and an indicator of its demographic future (Bullock *et al.* 1996, Condit *et al.* 1998). Woody plant size is considered to be of greater significance than age in determining population structure, fecundity and survival, with vital rates being size-dependent (Harper 1977, Caswell 1989). Although these data have the relative merit of being easily collected, it must be acknowledged that they are static ‘snapshot’ representations of population composition at a particular moment in time. Attempts to accurately estimate rates of change or to predict future changes are confounded as projections make

assumptions about the behaviour and identity of agents of change (Wiegand *et al.* 2000, Obiri *et al.* 2001). Additionally, changes in size-specific vital rates (e.g. growth, survival and fecundity), perhaps through growth suppression (e.g. by fire or browsers) or density dependence (competition and self-thinning), will alter population structure and may have consequences that reverberate down through generations (Caswell 1989, Condit 1998).

1.5.1.2 Plant functional groups and syndromes of regeneration

Plants within an environment are faced with the same constraints and opportunities. They therefore tend to converge on a limited number of functional types (Smith *et al.* 1997, Woodward *et al.* 1997). Functional group classification is therefore a context-specific simplification that has been used to predict the dynamics of systems. Such generalisations are the basis of both theoretical and applied ecology, supporting predictions of vegetation change from limited information. Plant functional types have therefore been an essential component of model development (McIntyre 1999). Functional groupings have been given a renewed emphasis by the need to predict the response of plants to substantial and rapid environmental changes at the global scale, such as changes in land use, climate and atmospheric composition (Scholes *et al.* 1997). Historically, influential approaches have included r- and K- strategists (Harper 1977), the CSR scheme (competitors, stress-tolerators and ruderals) (Grime 1977), and the resource-ratio hypothesis (Tilman 1988). These strategy schemes are the outcome of attempts to identify key biological features of plants that may be associated with success in habitats with particular patterns of resource availability. The success of individual species strategies in relationship to the alternative strategies adopted by co-occurring species determines their competitive ability in utilising limited resources and their persistence in the face of disturbance. The species dominating a particular area are therefore indicative of the relative importance of the factors and destructive agents that shape them (Archibald & Bond 2003). The designation of 'response groups' involves identifying a specific disturbance or environmental variable, identifying groups of species that respond to the variable

in similar ways and the biological attributes associated with the different response groups (McIntyre 1999).

1.5.1.3 Spatial modelling

"It may prove enlightening to take spatial pattern as an essential component of plant demography, rather than as an unfortunate barrier to reliable population estimates" (Crawley 1990).

Modelling is a valuable tool for exploring the spatial and temporal scales of population response to change. It supports the integration of existing data sets and an assessment of our present understanding of ecological processes (Dunning *et al.* 1995). A combination of field investigations and simulation modelling has the power to extract the maximum of information available within a short-term study (Wiegand *et al.* 2000). Grid-based models, such as the model conceived by this study, establish in a simple way the spatial context that governs interactions among plants. The environment is divided into a regular patch mosaic of cells with a focus on the processes of recruitment and establishment within each cell. Patch transitions depend on the current state of the cell and on the states of neighbouring cells. Spatially-explicit grid based models have been used effectively to gain an understanding of savanna functioning (Jeltsch *et al.* 1996, 1998, Higgins *et al.* 2000, Wiegand *et al.* 2000). These have also highlighted conspicuous gaps in our empirical understanding, including variation in woody plant recruitment opportunities and the importance of persistence following damage. The ability to model and examine ecological processes on a large landscape or ecosystem scale has particular relevance for the sustainable management of natural resources.

1.6 THESIS STRUCTURE

The chapters of this thesis, with the exception of the Introduction and Synthesis, are autonomous and written in the format of scientific papers to be submitted for publication in internationally recognised scientific journals (Chapter 5 has been accepted for publication by the journal of *Forest Ecology and Management*).

Presenting a thesis as a collection of papers for publication inevitably results in some repetition, particularly in the sections describing the study region and methods of data collection. To the reader of the thesis in its entirety, I apologise for this. Following this introductory chapter (which situates the study within a framework of prior research, and specifically in light of its regional context), each of the Chapters 2 to 5 tackles a study objective towards improving current understanding of the processes and determinants of savanna woodland regeneration. The findings of the study, contributing towards the formulation of the woodland simulation model described in Chapter 6, are integrated in the Synthesis chapter. This final chapter articulates the ecological and theoretical implications of the study's results and highlights those pertinent to savanna woodland conservation and its sustainable utilisation. Figure 3 (on page 17) depicts the structure of the thesis.

Chapter 2 lays the foundation of the study, examining the current status of savanna woody plant populations, both in woodlands under communal subsistence land use and in adjacent protected areas. The effects of live wood harvesting and other factors on woody plant demography, recruitment potential and resource sustainability are determined.

In *Chapter 3*, the emphasis shifts to an exploration of woody plant allometry and an examination of how savanna woody plant species differ in their 'growth strategy' in response to prevalent stresses. Previous research on woody plant allometry, growth strategies and population dynamics has largely focused on tropical rainforest species. Results are discussed in relationship to prevailing theories of tropical forest tree growth and population dynamics and the methods used to examine these.

Chapter 4 and *Chapter 5* form the core of the study's focus on the regeneration of savanna woodlands. *Chapter 4* examines the determinants of woody plant seedling establishment success. *Chapter 5* investigates the resprouting response of savanna woody plants following live wood harvesting.

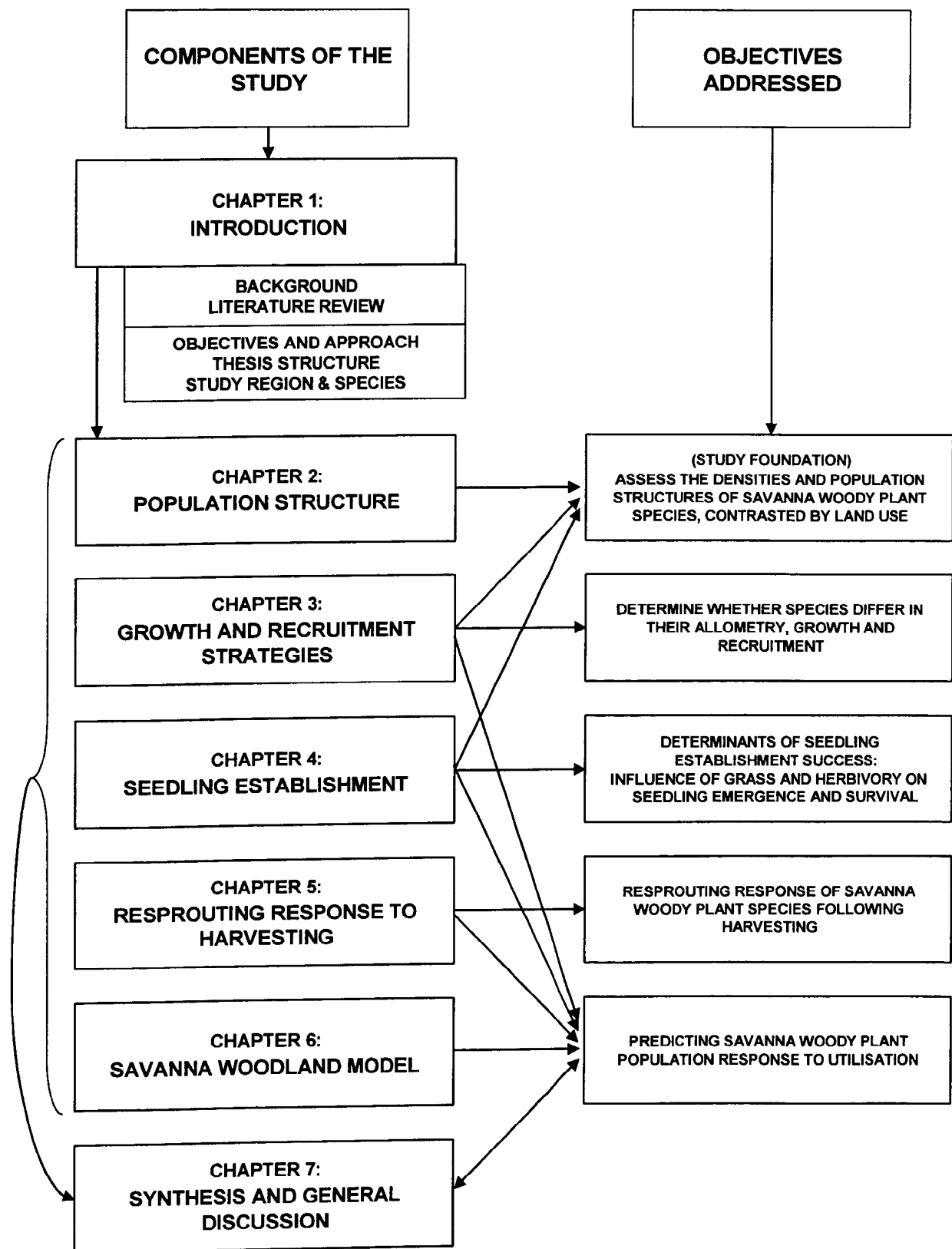


Figure 3. Study (thesis) structure for an investigation of the regeneration ecology of savanna woodlands in relationship to human utilisation.

Chapter 6 assimilates the empirical findings of the previous chapters through the formulation of a woodland model that simulates the population dynamics of woody plant populations in response to harvesting pressures. Model construction was a valuable process: synthesising current understanding, identifying key determinants and highlighting the gaps in our understanding of the system. The ultimate intention in the development of the woodland model is for it to be used as a tool, preferably by the resource users themselves, guiding sustainable live wood harvesting.

Chapter 7: the ecological and theoretical implications of the study's results, highlighting those pertinent to savanna woodland conservation and sustainable utilisation.

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CHAPTER 2

Savanna Woody Plant Demography: Contrasting the Effects of Protection and Communal Subsistence Land Use on Recruitment Potential and Resource Sustainability

Abstract

To guide the sustainable use of savanna woodland resources it is essential to understand how humans alter woody plant demography and recruitment potential. Densities and population structures of common savanna woody plant species were examined in land under communal tenure in the lowveld of South Africa and contrasted between adjacent state- and privately-owned protected areas. Aboveground live wood biomass was lower in communal rangelands than in protected areas. Overall population structure, as represented by 'functional' size class density distributions, differed significantly for most species between land uses, with woody plant densities of all size classes generally higher in protected areas. For *Terminalia sericea* there were considerably fewer 'small reproductive woody plants', i.e. 10 to 20 cm in stem diameter size, in communal rangelands than in protected areas. *T. sericea* and *Dichrostachys cinerea*, the species most frequently harvested, had significantly fewer reproductively 'mature' plants relative to 'immature' plants in communal rangelands than in protected areas. The plants of many species were more highly branched in communal rangelands than in protected areas, indicative of a resprouting response following damage. The combined seedlings of all species were at lower densities in communal rangelands than in protected areas, with the exception of the most intensively harvested site. Sampling along a gradient of decreasing woodland utilisation with distance from a settlement revealed a shift in woody plant population structure from predominantly short multi-stemmed plants close to the settlement, to a wider range in plant size and form with a higher live wood biomass further away. This study indicates that live wood harvesting within communal rangelands has significantly impacted on the demography of favoured species. Although most savanna woody plant species resprout following harvesting and no loss of species was observed, current levels of resource utilisation appear unsustainable with live wood biomass and recruitment potential considerably reduced and with little evidence of compensatory recruitment.

Keywords: fuelwood harvesting; natural resource management; resprouting; seedlings; size density distributions; woodlands

2.1 INTRODUCTION

Savanna woodlands provide the primary source of energy for the majority of South African rural households (Shackleton 1993). Within the Bushbuckridge region, fuelwood demand has been estimated to be in excess of 500 kg per person per annum, an amount predicted to be locally unsustainable over the next few decades (Griffin *et al.* 1992, Banks *et al.* 1996, Dovie *et al.* 2002). In recent years in this region, fuelwood harvesting has shifted from the collection of deadwood to include the cutting of live trees (Dovie *et al.* 2004). Indeed, as much as 93% of current demand is not met by available deadwood and is harvested unsustainably as live wood (Shackleton & Shackleton 2000). In general, the rate of fuelwood usage from woodlands in South Africa has not decreased despite attempts to introduce alternative energy sources (Dovie *et al.* 2004). With increasing populations, adverse crop growing conditions, high levels of poverty and few local employment opportunities, the pressures on woodlands will intensify. Effective management of natural resources is crucial to their sustained availability.

Much research has focused on the key determinants of savanna woody plant demography and specifically on the coexistence of woody plants and grasses that characterise savanna systems. The interactive effects of erratic rainfall, fire, herbivores and competition with grass whilst woody plants are still within the grass layer, are widely viewed as being the most influential in determining woody plant dynamics (Scholes 1997, Jeltsch *et al.* 1998, Higgins *et al.* 2000, Sankaran *et al.* 2004). Large-scale successional changes in savannas have been associated with human activity such as sustained grazing, wood harvesting and clearing for agriculture and settlement. Even in relatively ‘undisturbed savannas’, humans have indirectly influenced vegetation by altering fire regimes and the variety of browsers present (Huntley & Walker 1982, Scholes 1997). Communal rangelands, frequently characterised by a prolonged and intensive utilisation of woodlands by humans, provide a suitable context for investigating the consequences of this use for woody plant demography (Shackleton *et al.* 1994, Frost 1996).

Conservation policies for forests and woodlands have tended to focus on those species considered valuable for their timber or medicinal properties. These policies rarely include measures for examining the value of the broader spectrum of species for people's livelihoods and for monitoring their status (Dovie *et al.* 2004). Some overlooked species, including those commonly used for fuelwood, may be threatened with overexploitation. Their loss could impact the livelihoods dependent on them, may increase the pressure on other species and could conceivably impact ecosystem functioning.

Baseline information regarding the density and size composition of favoured woody plant species together with an understanding of their regenerative capacity is crucial for guiding effective conservation policies and practices to facilitate sustainable fuelwood harvesting (Seydack 1991, Everard *et al.* 1995, Neke 2002 (Appendix 1), Obiri *et al.* 2001). The study's primary objective was to examine whether live wood harvesting in communal rangelands has significantly influenced woody plant population dynamics and if so, whether there is evidence that this might jeopardise future resource availability. This objective was explored by contrasting the woodlands of communal rangelands with those of adjacent protected areas, as well as woodlands along a gradient of resource utilisation intensity. Specifically, in order to meet the primary objective, the study sought evidence of:

1. A reduced aboveground live wood biomass in communal rangelands relative to protected areas.
2. Changes in woody plant species composition with a possible absence of certain species in heavily harvested areas.
3. An altered demography of favoured woody plant species with the expectation that densities of plants of the sizes most frequently harvested would be lower in communal rangelands.
4. A reduced woody plant regenerative capacity with fewer large, seed-producing plants in communal rangelands relative to protected areas.
5. Fewer recently established plants in communal rangelands.

The implications of the study's findings for continued woodland resource availability are discussed.

2.2 STUDY REGION

2.2.1 Study area and land use

Within the Bushbuckridge region human population numbers are high. There are more than 300 people km⁻² in the west and 160 people km⁻² in the drier east. The region forms part of the former homeland areas of Gazankulu and Lebowa, with communal settlements imposed under the 1948 South African apartheid system (Pollard *et al.* 1999). Settlements differ in size and duration of habitation: Acornhoek is the largest and Thorndale, adjacent to the Manyeleti Reserve, the smallest and most recently inhabited in the late 1970s. Settlements are crowded, with land and water inadequate.

The term 'communal rangelands' refers to the vegetated land under communal tenure surrounding settlements. The main uses of this land are for livestock grazing and the harvesting of natural resources. Large-scale poverty has resulted in an accelerating depletion of natural resources. In particular the demand for fuelwood has outstripped the supply of natural dry wood and led to live wood harvesting (Shackleton & Shackleton 2000, Twine 2002). Prior to 1994 and South Africa's first democratic elections, there was some control over woodland resources with Tribal Authority chiefs and 'tribal police' controlling resource use and punishing infringers. Since then, control has largely degenerated into an 'open access' system, with external users adding to the rapid depletion of natural resources. Densities of wild herbivores within communal rangelands are negligible. Livestock grazing has reduced grass biomass and hence the frequency, intensity and extent of fires, especially in the rangeland areas surrounding settlements.

Following land under communal tenure, the second largest use of land in the Bushbuckridge region is for protected areas. Protected areas are state- or

privately-owned game reserves used for wildlife conservation, ecotourism and hunting. They differ in the time since proclamation and in their management, including of wild animal numbers and fire. Of the protected areas selected for the study, Wits Rural Facility has the most recent history of alternative land use having been used as a commercial cattle ranch prior to 1968 (Shackleton 1997). With the exception of Wits Rural Facility, protected area study sites have elephants and large browsers such as giraffe and kudu. Wits Rural Facility has lower densities of kudu and smaller herbivores such as impala. All protected areas follow fire management plans, burning on average every 3 to 5 years depending on fuel-load accumulation. There has been limited harvesting of natural resources within protected areas with neighbouring communities largely denied access to fuelwood and other resources.

2.2.2 Biophysical characteristics

The study region within the Bushbuckridge Lowveld of the Limpopo Province (centering on 31° 17' E; 24° 39' S) stretches east from the communal rangelands of Acornhoek settlement to the Manyeleti Reserve bordering the Kruger National Park (Figure 1 on page 30). Within the study region, the close proximity of many of the settlements to protected areas facilitated a comparison of the woodlands of communal rangelands with those of adjacent protected areas.

The region is characterised by low rainfall (ca. 650 mm per annum in the west; ca. 550 mm per annum in the east), concentrated in the summer season (October to May). This is mainly in the form of convectional thundershowers (Shackleton 1997). Intra-seasonal drought is common with more prolonged drought occurring as often as every 3.5 years. Mean annual temperature is 22° C. Mean daily maxima are approximately 30° C in January and 23° C in July (Pollard *et al.* 1999).

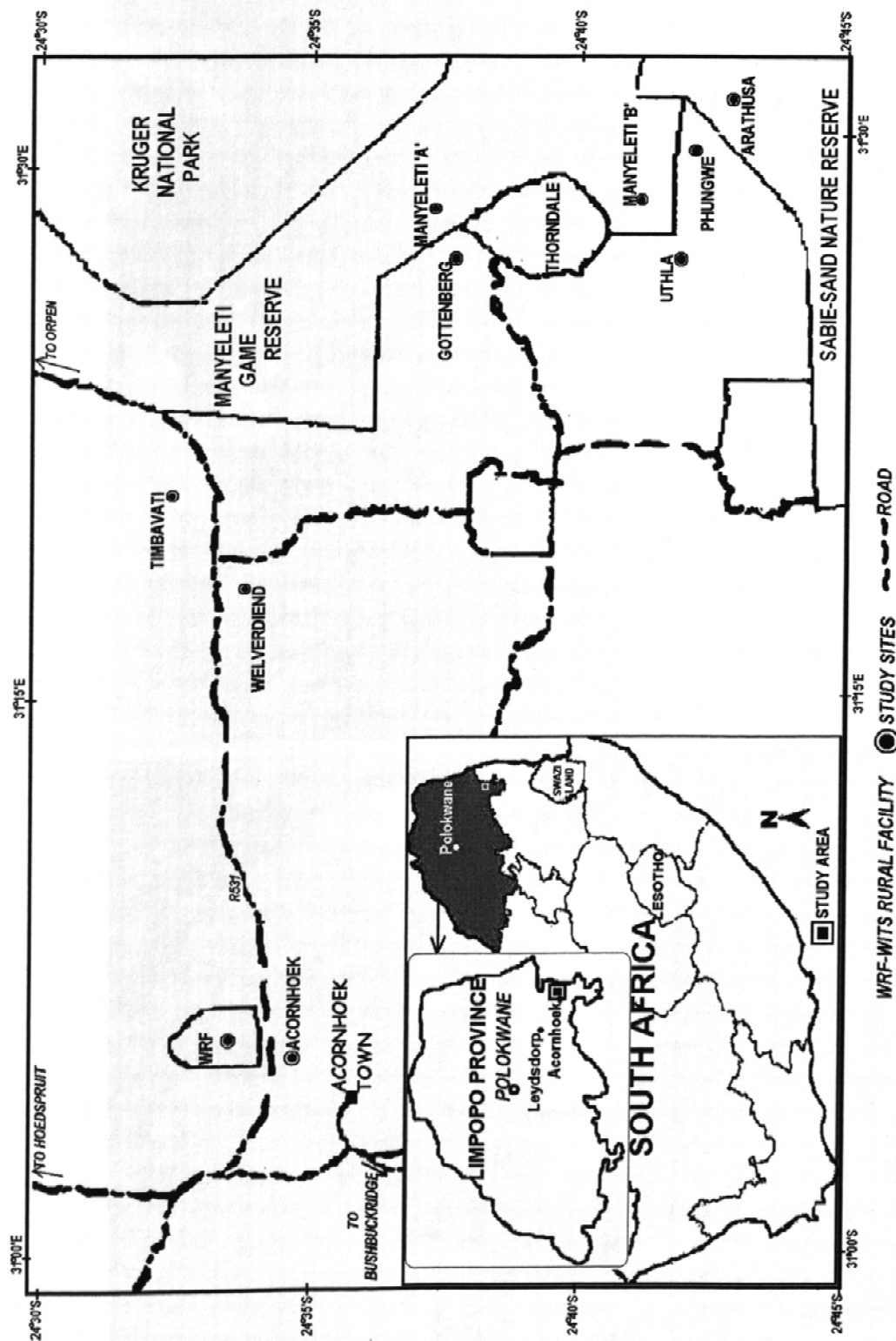


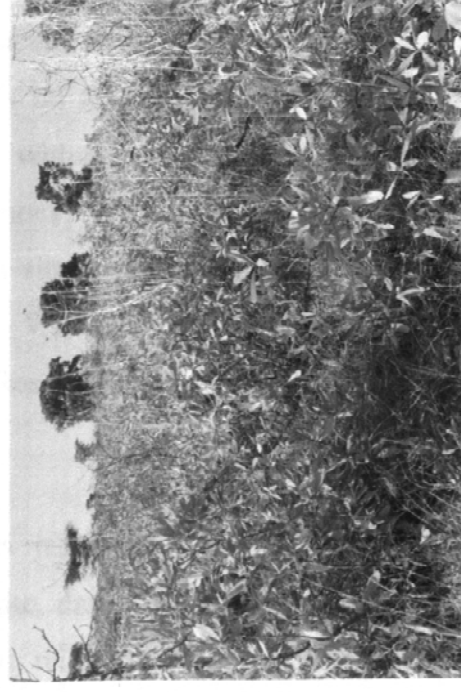
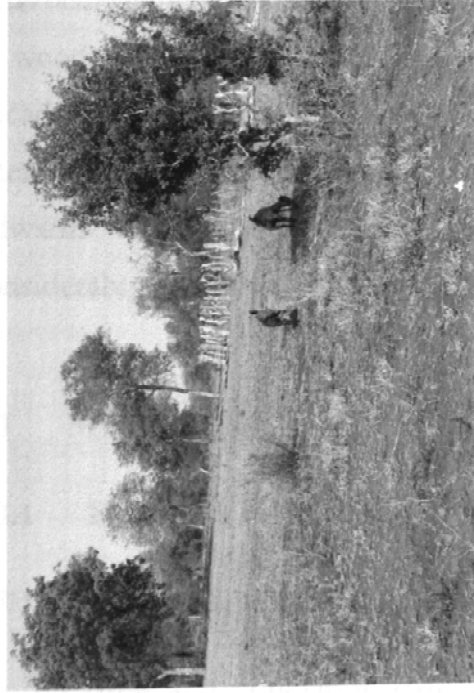
Figure 1. Map of the Bushbuckridge study region, Limpopo Province, South Africa. Paired study sites in communal rangelands and protected areas are indicated. Additional sampling was carried out in the woodlands surrounding Thorndale.



Left: Photograph taken in Arathusa within the Sabie Sand Game Reserve, with marulas *Sclerocarya birrea* in the background, a red bushwillow *Combretum apiculatum* to the right and good grass cover (primarily *Panicum maximum*) in the foreground.



Above: Photograph taken in Wits Rural Facility, another of the protected area study sites, with silver clusterleaf *Terminalia sericea* trees dominating the woody component and yellow thatching grass *Hyperthelia dissoluta* visible in the herbaceous cover.



Top left: Images of communal rangelands during a particularly dry season, showing little grass cover and few woody plants. *Top right:* grazing goats and a cattle kraal close to Thorndale settlement. *Bottom left:* *Terminalia sericea* trees close to Acomhoek settlement, browsed by livestock and 'trapped' within the grass layer. *Bottom right:* the communal rangelands of Welverdiend settlement during a wetter period, with grazing cattle in the foreground and houses in the background. The emergent trees are marulas *Sclerocarya birrea*.

The topography of the study region is gently undulating. Soils are underlain by granitic gneiss with local intrusions of gabbro. Vegetation of the region is broadly classified as Mixed Lowveld Bushveld and is dominated by species of the Combretaceae (Van Rooyen & Bredenkamp 1996). Additionally, the marula *Sclerocarya birrea* and sickle bush *Dichrostachys cinerea* contribute considerably to woody biomass within the region (Shackleton 1997). There have been several decades of intensive utilisation of communal grazing lands resulting in an alteration of woodland structure described as “short sparse woodland” by Edwards’ (1983) physiognomic classification. Adjacent protected areas have considerably denser woody vegetation and are classified as “short bushland”.

2.3 METHODS

2.3.1 Field data collection

2.3.1.1 Land use contrast

The densities and population structure of woody plant species were compared within communal rangelands and adjacent protected areas. All study sites were located within broad-leaved woodlands on the relatively level ground of upland areas. Five sites were positioned within the communal woodland areas surrounding the settlements of Acornhoek, Welverdiend, Gottenberg, Utlha and Phungwe and each was paired with a site located less than 2 km away, in the woodlands of adjacent protected areas - Wits Rural Facility, Timbavati, Manyeleti (two sites) and the Sabie Sand Game Reserve, respectively. Altitude at all sites is approximately 450 to 550 m a.s.l.

Fifteen common woody plant species were selected, representing a range of growth forms (Appendix 2). At each site, data were collected along eight 100 m long transects comprising two sampling widths: 4 m wide for woody plants less than 4.5 m in height and 40 m wide for those more than 4.5 m in height, these being far fewer. Transects were positioned: (i) with the long axis along a north-south compass bearing, (ii) for communal rangelands, in woodlands that had not been cleared for agricultural fields, appearing ‘relatively intact’ to the eye and

(iii) for both communal rangeland and protected areas, as systematically and equidistantly as possible within the wooded area.

The information recorded for the selected woody plant species included: species, plant height (height of the tallest live stem) and basal stem diameter (measured close to the ground or just above the basal swelling when present). For multi-stemmed plants, the diameters of all stems were measured. If the woody plant had been harvested, i.e. its aboveground biomass cut and removed, the proportion of the plant harvested was recorded, following Walker's (1976) ranking scale (1: 0-10% of the plant's aboveground biomass harvested; 2: 11-25%; 3: 26-50%; 4: 51-75%; 5: 76-90%; 6: 91-99%; and 7: the entire plant having been cut with only a stump remaining). For woody plants that had been entirely harvested, remaining stumps were identified to species by distinguishing bark, wood, symmetry or resprout growth and their diameters measured.

2.3.1.2 Rangeland utilisation gradient

Additional sampling was undertaken within the communal rangelands of Thorndale. By sampling with increasing distance from the settlement, trends in woody plant demography associated with woodland resource utilisation intensity could be detected. Thorndale is one of the most remote of the settlements in the study region and consequently woodland resource use has been primarily by residents with little 'outsider' influence (Giannecchini 2001). The land surrounding Thorndale is zoned into arable and residential plots with the remainder used as grazing lands and for the extraction of natural resources such as fuelwood, thatching grass, construction materials and fruits (Dovie *et al.* 2002). The population has been estimated to be 450 people in 71 households. Of these, 96% of households use fuelwood as their sole source of energy (Dovie *et al.* 2002), with mean annual consumption estimated to be 4343 ± 333 kg per user household (Dovie *et al.* 2004), i.e. 685 ± 53 kg per person. Livestock numbers were estimated to be approximately 380 cattle and 130 goats (Dovie *et al.* In Press), with numbers fluctuating in response to variable rainfall.

Following Shackleton *et al.* (1994), sampling took the form of three transects radiating outwards from the settlement, with each transect consisting of three plots. The plot closest to the settlement of each transect was situated approximately 350 m from the edge of the settlement (last field or residential stand). The far plot was positioned approximately 1 km from the settlement, along a pre-determined bearing relative to the near plot and was situated in a stand of relatively undisturbed vegetation (representing the highest density of woody plants available to fuelwood harvesters). The mid plot was situated mid-way between the near and far plots. Each plot consisted of a belt transect, 4 m x 100 m, with the long axis placed along the transect line. The previously described information was recorded for all woody plants of all species. Herbaceous cover, i.e. grass biomass and prevalent grass species, was recorded in each plot.

2.3.2 Data Analysis

All analyses were undertaken at the plant level. For multi-stemmed plants, total stem diameter was determined by calculating the cross-sectional areas of all composite stems ($a = \pi \times (0.5 \times d)^2$), summing them and using this aggregate stem area to calculate the effective stem diameter for each tree.

2.3.2.1 *Woody plant densities and live wood biomass*

The number of woody plants sampled per species was converted to density per hectare taking into account the two-width transect sampling design. Overall densities of all woody plant species were not determined as non-selected species had only a minor representation at each site. In determining the densities and relative abundance of the study species, seedlings and root suckers, i.e. woody plants with a stem diameter less than 1 cm (hereafter referred to as seedlings) were excluded as these may not have been established and would therefore be vulnerable to higher levels of mortality.

The aboveground live wood biomass (B) for each site was determined from woody plant stem diameters (D) (cm), using the equation of Netshiluvhi & Scholes (2002) for broad-leafed species:

$$B \text{ (t ha}^{-1}\text{)} = \sum_{i=1}^n 0.035 D_i^{2.5},$$

where n is the number of sites, i is the number of woody plants in each site and D_i is the stem diameter of each woody plant. For woody plants that had been partially harvested, remaining wood biomass was calculated using the proportion of the plant's former total stem diameter left behind (100% – the range midpoint of the proportion harvested, multiplied by the former total stem diameter). A Wilcoxon matched pairs test determined whether live wood biomass within communal rangelands differed significantly from the live wood biomass of protected areas.

The species and size composition of harvested woody plants was assessed to determine whether resource users had actively selected particular species and size plants. For plants that had been partially harvested, the cut diameter was calculated as the proportion of the plant's former total stem diameter harvested (again using the range midpoint of the proportion harvested).

2.3.2.2 Woody plant population structure

The population structure of each species was represented as woody plant density per hectare, for each of the following 'functional' stem diameter categories (following Luoga *et al.* 2000a, 2000b, 2002):

- 0 to < 1 cm: considered to represent new regeneration by 'seedlings' or 'resprouts' (referred to here as root suckers);
- 1 to < 4 cm: 'saplings';
- 4 to < 10 cm: 'poles';
- 10 to < 20 cm: 'small reproductive woody plants';
- ≥ 20 cm: 'large reproductive woody plants'.

Woody plants with less than 25% of their aboveground biomass harvested were included in the stem diameter distributions. Plants with a larger proportion of their

aboveground biomass harvested were not represented in stem diameter distributions, with the assumption that their growth and reproductive functioning would be considerably altered and their survivorship unknown.

Kolmogorov-Smirnov tests, contrasting stem diameter distributions, were used to assess whether overall population structure had been significantly altered in communal rangelands as a result of human utilisation. The woody plant densities of particular functional size categories were compared between land uses, using Wilcoxon matched pairs tests of the five paired communal rangeland and protected area sites. Postulates tested were that within communal rangelands:

- Woody plant densities within the size categories most frequently harvested would be lower than in protected areas.
- Harvested populations would have fewer mature seed-producing plants.
- The number of seedlings would be lower as a result of livestock browsing and trampling, seed limitation and unfavourable recruitment conditions.

In an adaptation of the methods used by Everard *et al.* (1995) and Obiri *et al.* (2001), woody plant recruitment potential was assessed by comparing the ratio of reproductively immature to mature plants of each woody plant species population under alternate land uses. Following Shackleton (1997), mature plants, i.e. potentially seed-bearing, were defined as those taller than two thirds of the maximum height of that species (calculated as the mean of the ten tallest plants). Remaining plants were defined as immature, excluding plants less than 1 cm in diameter considered to be seedlings that may not yet have been fully established. These species-specific heights at maturity were all greater than 3 m and above flame height, the minimum height at which savanna trees in general are considered to produce seeds (Archibald & Bond 2003). Chi-square tests with Yates correction were used to assess whether the proportion of immature and mature woody plants composing populations differed between communal rangelands and protected areas. The number of stems per plant under either land use was compared using a Mann-Whitney U test.

2.3.2.3 *Rangeland utilisation gradient*

Woody plant dimensions, i.e. diameter, height and stem number per plant, were tested for normality with Shapiro-Wilk's W tests, following which changes with distance from the settlement were assessed using non-parametric Kruskal-Wallis median tests. Plants with evidence of having been cut were excluded from the analysis. Live wood biomass, woody plant (≥ 1 cm in stem diameter) and seedling (< 1 cm in stem diameter) densities and the proportion and density of woody plants with evidence of harvesting, were contrasted for near, mid and far sites, using Kruskal-Wallis tests. Population structures were represented using the previously described stem diameter categories.

2.4 RESULTS

2.4.1 Live wood biomass and woody plant densities

Standing live wood biomass was significantly higher in protected areas (median = 18.21 t ha⁻¹; SD $\pm$ 5.39 t ha⁻¹) than in communal rangelands (median = 14.97 t ha⁻¹; SD $\pm$ 5.6 t ha⁻¹) (Wilcoxon matched pairs test: $z = 2.203$, $P < 0.05$, degrees of freedom (d.f.) = 4).

Each study species was present under both land uses. The relative abundance of the study species, excluding seedlings, differed between communal rangelands and protected areas, with *Combretum apiculatum* being the most abundant (relatively and absolutely) in communal rangelands, followed by *Strychnos madagascariensis*, *Terminalia sericea* and *Dichrostachys cinerea* (Figure 2 on page 39, Table 1 on page 40). In protected areas, *T. sericea* and *D. cinerea* occurred at higher relative abundances than both *S. madagascariensis* and *C. apiculatum*.

Of the woody plants sampled within communal rangelands, 12.9% had evidence of harvesting with all or some stems cut, in contrast to 0.9% of those in protected areas. Within communal rangelands, cut woody plants largely comprised

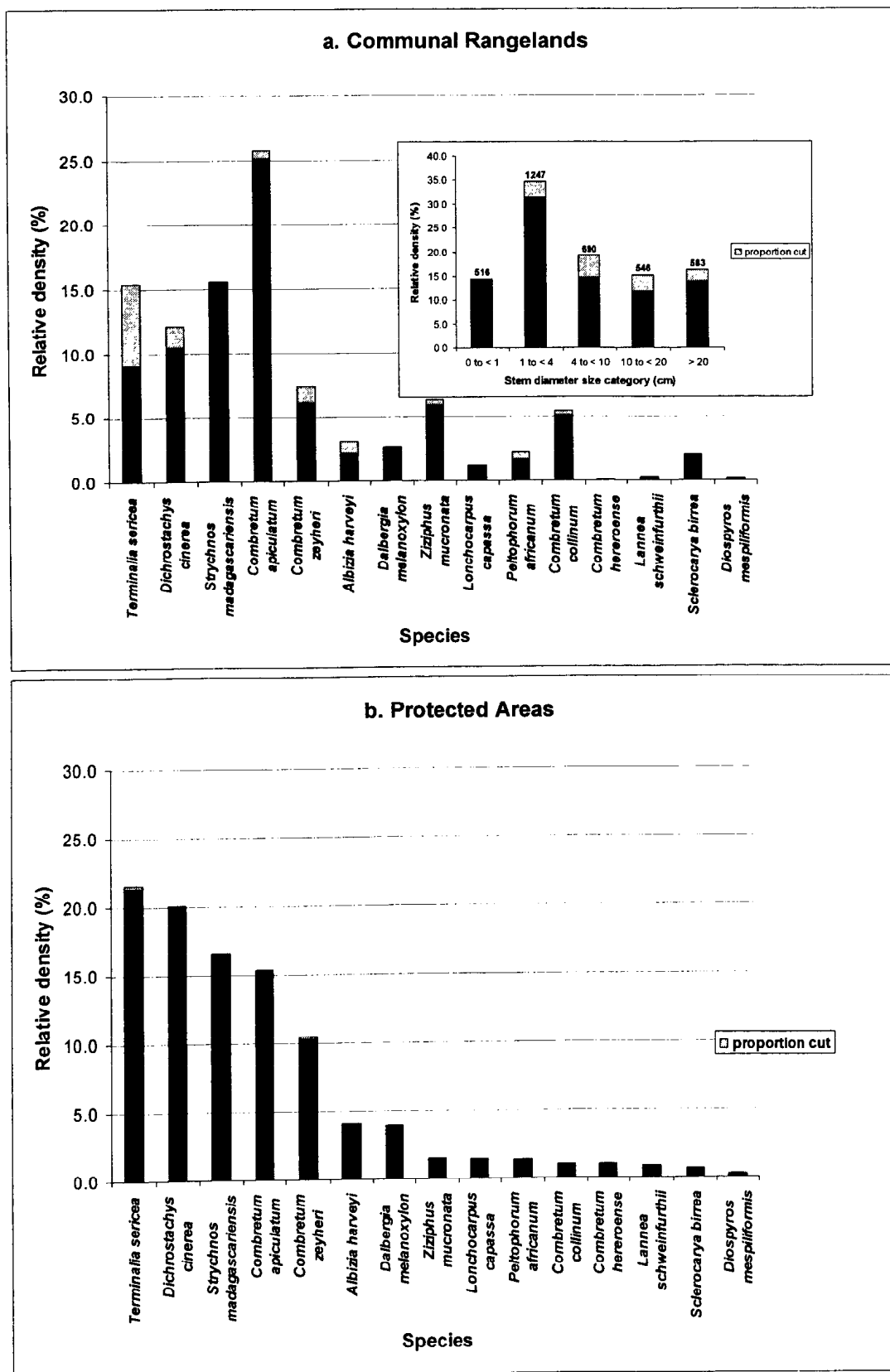


Figure 2. Relative density (trees per hectare) of selected woody plant species in (a) communal rangelands and (b) protected areas, with the proportion of plants showing evidence of harvesting. Seedlings and resprouts (< 1 cm in stem diameter) were excluded. Inset in (a) shows the size frequency distribution of all woody plants combined, with the proportion of each stem diameter size class harvested (sample sizes above bars).

Table 1. Woody plant densities (per hectare) in communal rangelands and protected areas, with the species composition of cut woody plants. Total for woody plant density is for the combined study species and excludes seedling densities.

SPECIES	COMMUNAL			PROTECTED		
	Woody plant density (ha ⁻¹) (± SD)	Composition of cut plants (%)	n	Woody plant density (ha ⁻¹) (± SD)	Composition of cut plants (%)	n
<i>Terminalia sericea</i>	205 (± 189)	49.8	380	219 (± 250)	13.3	1095
<i>Dichrostachys cinerea</i>	129 (± 150)	13.1	255	385 (± 305)	19.0	636
<i>Strychnos madagascariensis</i>	244 (± 199)	1.4	351	304 (± 244)	0.0	396
<i>Combretum apiculatum</i>	463 (± 305)	4.6	813	221 (± 192)	11.0	743
<i>Combretum zeyheri</i>	97 (± 82)	10.1	344	86 (± 137)	16.7	512
<i>Albizia harveyi</i>	52 (± 36)	7.5	124	59 (± 53)	4.8	104
<i>Dalbergia melanoxylon</i>	32 (± 35)	1.0	76	57 (± 55)	15.7	141
<i>Ziziphus mucronata</i>	119 (± 74)	3.1	234	12 (± 16)	11.9	120
<i>Lonchocarpus capassa</i>	15 (± 24)	1.0	48	14 (± 30)	0.5	63
<i>Peltophorum africanum</i>	33 (± 29)	4.4	56	10 (± 10)	0.5	56
<i>Combretum collinum</i>	124 (± 83)	2.7	181	21 (± 37)	0.5	69
<i>Combretum hereroense</i>	13 (± 13)	0.0	7	28 (± 30)	4.8	35
<i>Lannea schweinfurthii</i>	3 (± 3)	0.2	32	11 (± 7)	1.0	44
<i>Sclerocarya birrea</i>	23 (± 22)	0.5	180	10 (± 14)	0.5	188
<i>Diospyros mespiliformis</i>	2 (± 5)	0.5	11	53 (± 46)	0.0	19
TOTAL	1247 (± 431)	100.0	3092	1429 (± 382)	100.0	4221

T. sericea (49.8%), *D. cinerea* (13.1%), *Combretum zeyheri* (10.1%) and *Albizia harveyi* (7.5%). Most heavily impacted on were *T. sericea* (41.5% of sampled plants cut), *A. harveyi* (30.9%), *Diospyros mespiliformis* (27.7%), *Peltophorum africanum* (25.4%), *C. zeyheri* (17.6%) and *D. cinerea* (13.9%). Despite being the most abundant species, relatively fewer *C. apiculatum* plants (2.3% of sampled plants) had been harvested. *S. madagascariensis* and *Sclerocarya birrea* had also been little harvested within communal rangelands (1.2% and 3.3% of sampled plants cut, respectively). Within protected areas, cut woody plants comprised mostly *D. cinerea* (19%), *C. zeyheri* (16.7%) and *Dalbergia melanoxylon* (15.7%).

Smaller stems had been cut in communal rangelands (median = 8.16 cm; SD $\pm$ 9.26 cm; n = 498) than in protected areas (median = 13.19 cm; SD $\pm$ 8.79 cm; n = 102) (ANOVA: $F_{1,598} = 4.47$, $P < 0.01$, d.f. = 4). In communal rangelands, the size frequency distribution for all cut woody plants combined indicated that the highest proportion of harvested woody plants were 4 to < 10 cm in stem diameter size (4.6% of woody plants of this size cut), followed by woody plants of diameter size 10 to < 20 cm (3.4%) and 1 to < 4 cm (3.3%). Of the woody plants larger than 20 cm in stem diameter, 2.4% had been harvested and only 0.2% of the woody plants of 0 to < 1cm in stem diameter size had been cut.

2.4.2 Woody plant population structure

The population size class structures of nine of the 15 study species differed significantly between communal rangelands and protected areas (Figure 3 on pages 42-44, Table 2 on page 45). For the majority of species, woody plant densities were higher in protected areas than in adjacent communal rangelands for all stem diameter categories. Notable exceptions were *Ziziphus mucronata* and *Combretum collinum*, with a higher density of plants in all stem diameter categories in communal rangelands than in protected areas (there were more *C. collinum* seedlings in protected areas than in communal rangelands). Median stem diameters for most species were greater in protected areas.

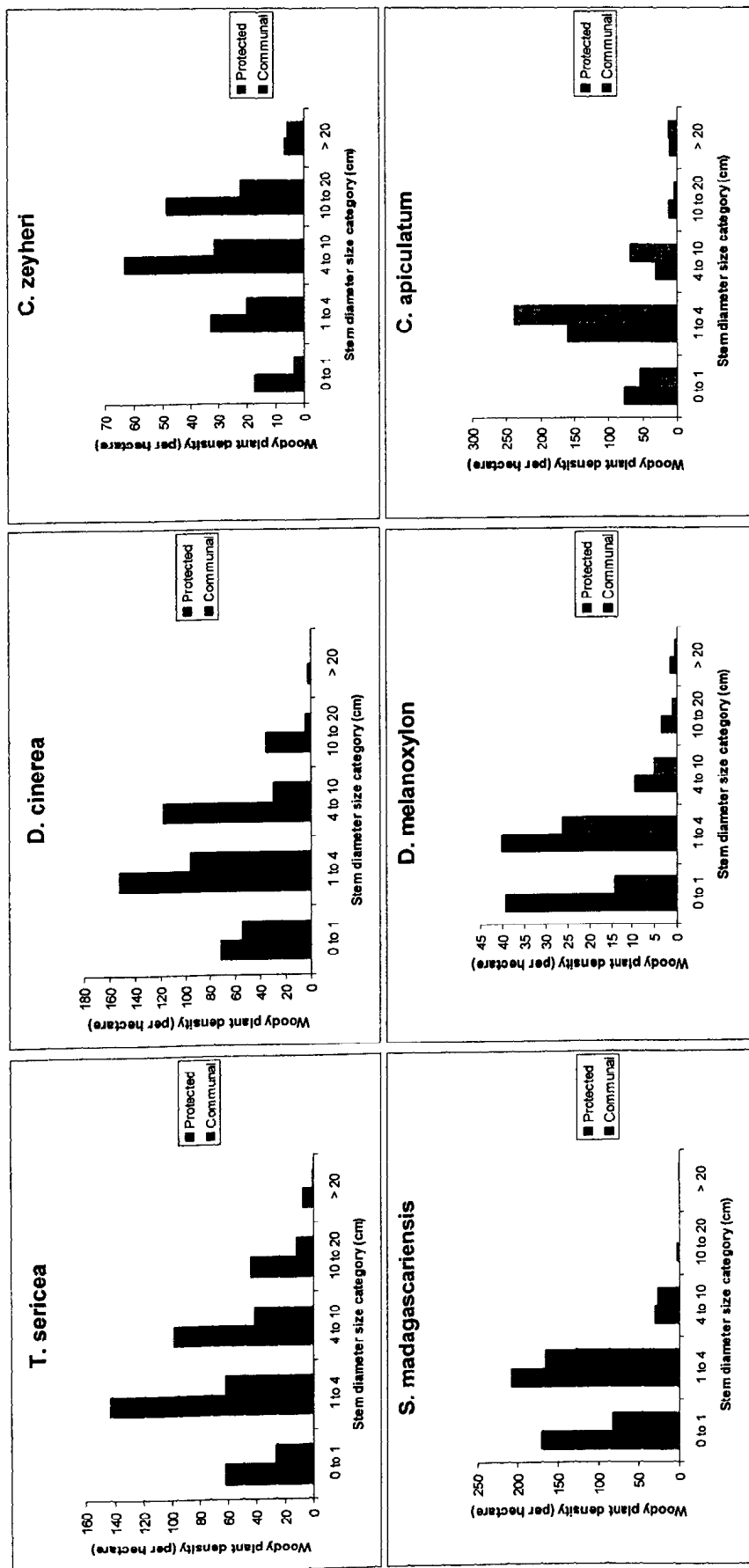


Figure 3. Contrasting stem diameter distributions representing population structure, for each study species, for communal rangelands and protected areas.

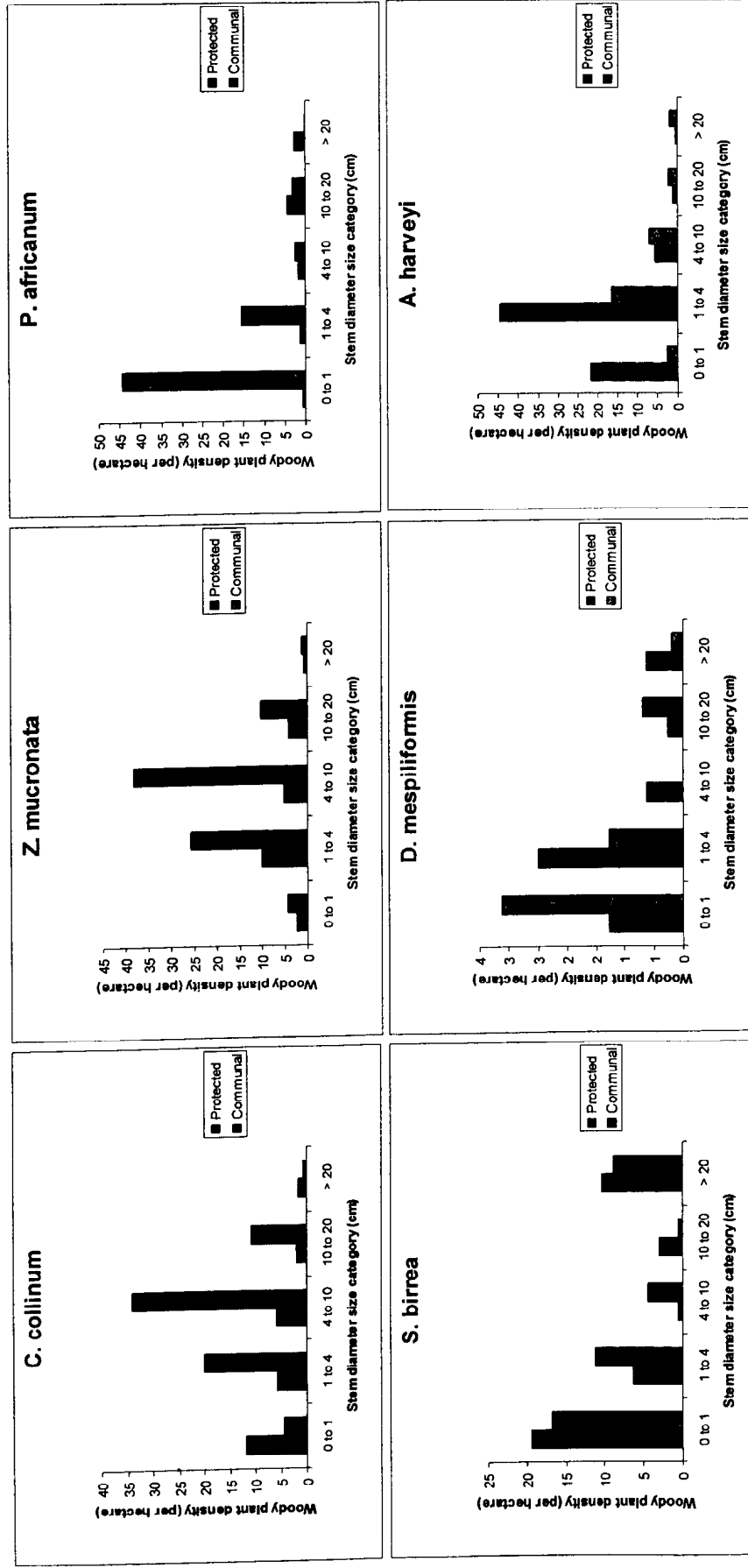


Figure 3 (continued). Contrasting stem diameter distributions representing population structure, for each study species, for communal rangelands and protected areas.

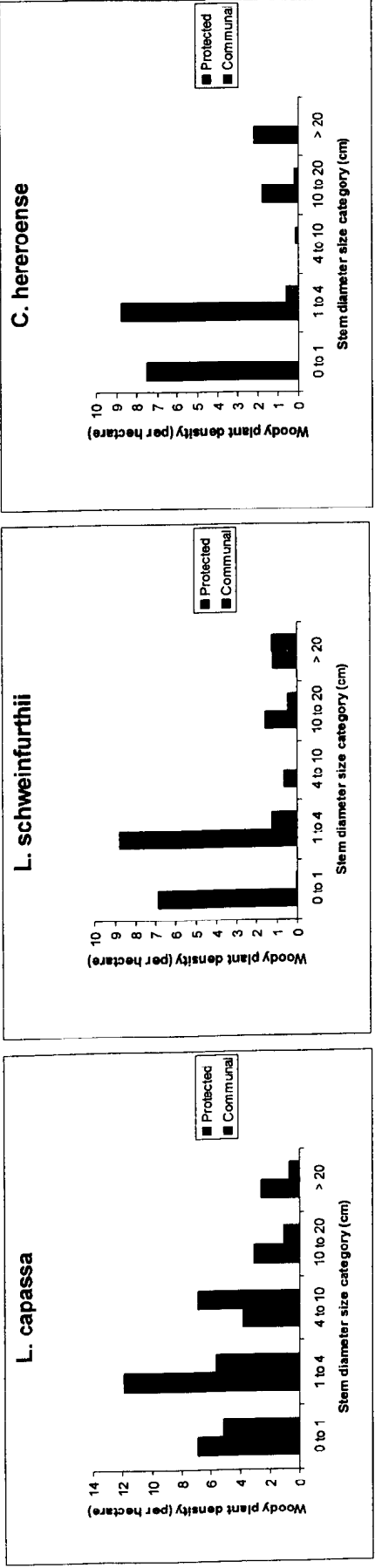


Figure 3 (continued). Contrasting stem diameter distributions representing population structure, for each study species, for communal rangelands and protected areas.

Table 2. Kolmogorov-Smirnov (KS) test results of statistical difference in population size class distributions (Bold P < 0.05), with median stem diameters for protected areas and communal rangelands.

Species	Protected		Communal		KS Statistical Parameters	
	median stem diameter ± SD (cm)	n	median stem diameter ± SD (cm)	n	D	P
<i>Terminalia sericea</i>	9.9 ± 7.6	1177	3.7 ± 7.8	266	0.34	< 0.0001
<i>Dichrostachys cinerea</i>	4.2 ± 5.7	737	1.9 ± 2.5	296	0.34	< 0.0001
<i>Combretum zeyheri</i>	12.73 ± 7.7	528	14.5 ± 8.2	296	0.09	> 0.05
<i>Strychnos madagascariensis</i>	1.17 ± 3.1	665	1.6 ± 7.9	467	0.21	< 0.0001
<i>Dalbergia melanoxylon</i>	6.0 ± 8.5	185	5.6 ± 7.8	91	0.10	> 0.1
<i>Combretum apiculatum</i>	10.9 ± 6.0	828	9.5 ± 3.3	831	0.17	< 0.0001
<i>Combretum collinum</i>	12.3 ± 17.2	88	8.2 ± 10.2	174	0.35	< 0.0001
<i>Ziziphus mucronata</i>	12.2 ± 7.5	108	8.8 ± 6.5	224	0.28	< 0.0001
<i>Peltophorum africanum</i>	23.5 ± 12.3	56	0.6 ± 6.6	109	0.84	< 0.0001
<i>Sclerocarya birrea</i>	31.4 ± 18.9	218	31.7 ± 21.8	202	0.10	> 0.1
<i>Diospyros mespiliformis</i>	18.8 ± 20.8	21	1.5 ± 19.8	12	0.49	> 0.05
<i>Albizia harveyi</i>	1.6 ± 6.9	129	7.5 ± 13.3	77	0.49	< 0.0001
<i>Lonchocarpus capassa</i>	8.6 ± 18.1	73	5.0 ± 11.2	49	0.13	> 0.1
<i>Lannea schweinfurthii</i>	14.3 ± 9.0	52	22.5 ± 22.3	30	0.42	< 0.01
<i>Combretum hereroense</i>	2.2 ± 12.2	44	9.5 ± 4.7	6	0.55	> 0.05

An examination of size density distributions shows most species to have a higher density of seedlings in protected areas than in communal rangelands, the exceptions being *P. africanum* and *D. mespiliformis*. Seedling densities were however highly variable between sites representing either land use. When species were tested individually for differences in seedling densities using paired adjacent sites as replicates, only *A. harveyi* and *Lannea schweinfurthii* were found to have significantly more seedlings within protected areas than in communal rangelands (Wilcoxon matched pairs test: $z = 2.023$, $P < 0.05$, d.f. = 4, for both). *C. zeyheri* and *D. melanoxylon* ‘tended’ to have more seedlings in protected areas ($z = 1.75$, $P = 0.08$, d.f. = 4, for both). Acornhoek, the most intensively harvested of the communal rangeland sites, had a higher density of seedlings for the species present, with the exception of *C. collinum*, than the adjacent protected area (Wilcoxon matched pairs test for all study species combined, using adjacent study sites as replicates: $z = 1.96$, $P < 0.05$, d.f. = 4), higher in fact than for any of the protected area sites. When this pair of sites was removed from the analysis, the seedling density, for all species combined, was significantly higher in protected areas than in communal rangelands ($z = 2.023$, $P < 0.05$, d.f. = 3).

T. sericea of 10 to < 20 cm in stem diameter size, i.e. ‘small reproductive woody plants’, were found at lower densities in communal rangelands relative to protected areas (Wilcoxon matched pairs test: $z = 2.023$, $P < 0.05$, d.f. = 4). *T. sericea* also ‘tended’ to have lower densities within the 4 to < 10 cm and 1 to < 4 cm stem diameter size categories ($z = 1.75$, $P = 0.08$, d.f. = 4 for both). *Lonchocarpus capassa* had a significantly higher density of 1 to < 4 cm diameter size plants in protected areas than in communal rangelands ($z = 2.023$, $P < 0.05$, d.f. = 4).

T. sericea and *D. cinerea*, the species most frequently harvested, had populations within communal rangelands with significantly fewer reproductively ‘mature’ plants relative to ‘immature’ plants than populations within protected areas (Chi-square = 6.94, $P < 0.01$, Chi-square = 5.45, $P < 0.05$, d.f. = 4, respectively).

The number of stems per plant was influenced by land use for several species. *T. sericea*, *D. cinerea*, *C. apiculatum*, *Z. mucronata* and *Combretum hereroense* plants had significantly more stems in communal rangelands than in protected areas, with *T. sericea* and *D. cinerea* plants of intermediate size more likely to have multiple stems (Figure 4 on page 48). *T. sericea* showed the clearest pattern, with plants in protected areas of all diameter sizes being single stemmed whilst those in communal rangelands were mostly three or four stemmed. The largest *T. sericea* plants (> 20 cm in stem diameter) were single stemmed in both communal rangelands and protected areas. In contrast, *D. cinerea* plants in protected areas were progressively more multi-stemmed with increasing size. *C. zeyheri* was the only species with significantly more stems per plant in protected areas. Many of the species for which there was no significant difference in stem number per plant with land use were single or at the most double stemmed for all size categories e.g. *Sclerocarya birrea*, *L. capassa*, *D. mespiliformis* and *L. schweinfurthii*. Species with a more branched growth form were *P. africanum* (median stem number = 3.3; SD $\pm$ 2.9) and *S. madagascariensis* (median stem number = 3.8; SD $\pm$ 3.4), both with a highly variable stem number that did not differ significantly with land use.

2.4.3 Rangeland utilisation gradient

Live wood biomass, for all woody plants combined, increased significantly with distance from the settlement with a median of 5.58 (SD $\pm$ 2.68) t ha⁻¹ at the near site, 7.86 (SD $\pm$ 1.0) t ha⁻¹ at the mid site and 17.14 (SD $\pm$ 2.73) t ha⁻¹ at the far site (Table 3 on page 49). Of the woody plants recorded in the near sites 30.4% (SD $\pm$ 18.3%) had been cut in contrast to 16.7% (SD $\pm$ 12.9%) at the mid sites and 6.5% (SD $\pm$ 3.2%) at the far sites. The number of species recorded did not differ in relationship to distance from the settlement, with the majority of species common to all sites. Woody plants closer to the settlement were significantly shorter in height, were more branched and had a smaller composite stem diameter than those further away. There was a trend of increasing woody plant and seedling density with distance from the settlement.

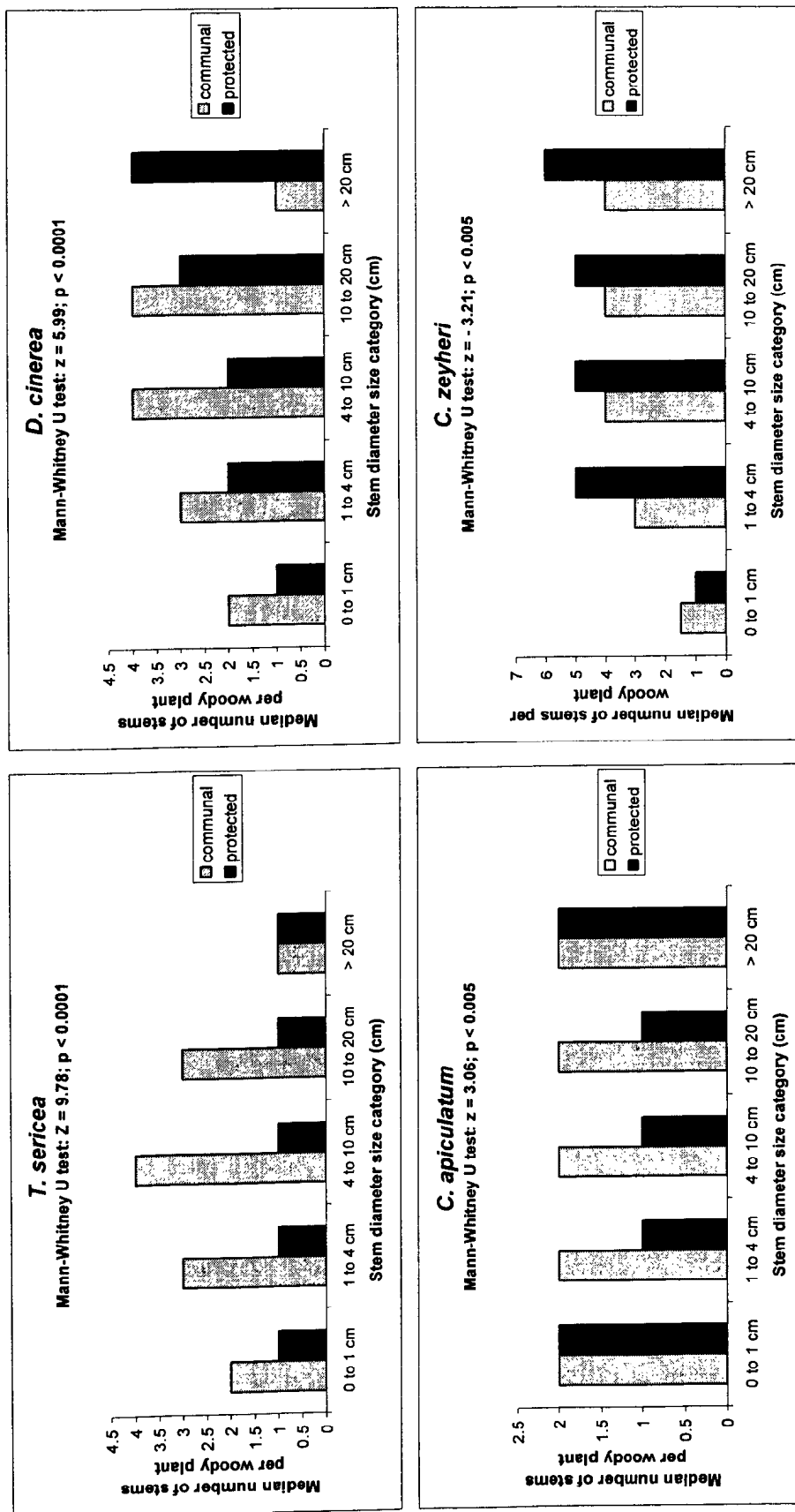


Figure 4. The median number of stems per woody plant within each diameter size category for communal rangelands and protected areas. Mann-Whitney U test results of significant difference are given.

Table 3. Comparison of woody plant parameters ($\pm$ SD) within communal rangelands, along an utilisation gradient with (plot) distance from Thorndale settlement (Bold $P < 0.05$). Kruskal-Wallis (KW) test results are given.

PLOT DISTANCE				
	Near (n = 225)	Mid (n = 456)	Far (n = 363)	Statistical Parameters KW Chi-square (df=2) P
Woody plant parameters				
<i>median</i> Height (m)	1.0 $\pm$ 1.2	1.8 $\pm$ 1.4	2.0 $\pm$ 1.8	52.8 < 0.0001
<i>median</i> Stem diameter (cm)	1.3 $\pm$ 3.5	3.0 $\pm$ 3.2	2.3 $\pm$ 4.8	21.4 < 0.0001
<i>median</i> Stem number per plant	2.0 $\pm$ 3.5	1.0 $\pm$ 1.7	1.0 $\pm$ 1.6	37.7 < 0.0001
Woodland parameters				
Aboveground livewood biomass (t. ha ⁻¹)	5.58 $\pm$ 2.68 (n = 132)	7.86 $\pm$ 1.0 (n = 323)	17.14 $\pm$ 2.73 (n = 254)	6.3 < 0.05
Woody plant density (no. ha ⁻¹)	366.7 $\pm$ 389.8 (n = 132)	897.2 $\pm$ 726.8 (n = 323)	705.6 $\pm$ 121.4 (n = 254)	0.9 > 0.5
Seedling density (no. ha ⁻¹)	258.3 $\pm$ 28.9 (n = 93)	369.4 $\pm$ 213.2 (n = 133)	300.0 $\pm$ 109.3 (n = 108)	0.9 > 0.5
Density of cut woody plants (no. ha ⁻¹)	100 $\pm$ 33.3 (n = 36)	116.7 $\pm$ 54.7 (n = 42)	47.2 $\pm$ 22.0 (n = 17)	3.6 > 0.1
Proportion of woody plants cut (%)	30.4 $\pm$ 18.3 (n = 36)	16.7 $\pm$ 12.9 (n = 42)	6.5 $\pm$ 3.2 (n = 17)	3.6 > 0.1

The size density distributions, for all woody plants combined and for species with sufficiently large sample sizes, showed a similar pattern: sites near to the settlement were dominated by small plants less than 4 cm in stem diameter, whilst sites further from the settlement had a wider range of sizes, including more seedlings and large plants (Figure 5 on page 51). For *C. zeyheri*, *C. collinum*, *C. apiculatum* and *Acacia nigrescens*, there were noticeably fewer seedlings near the settlement than at sites further away. In contrast, *Euclea divinorum* and *Acacia exuvialis* individuals sampled close to the settlement were predominantly seedlings.

2.5 DISCUSSION

Live wood biomass within communal rangelands was considerably lower than in the adjacent protected areas. Reduced live wood biomass results in a lowered production of deadwood (Shackleton 1998), important for sustainable wood harvesting. The study species most heavily harvested within communal rangelands were the most common within the study region and no loss of species as a result of harvesting had occurred. Their relative abundance differed between land uses, indicating a shift in species dominance in response to harvesting pressures. *Terminalia sericea* and *Dichrostachys cinerea*, the species most frequently harvested, were relatively more abundant in protected areas than in communal rangelands. *Combretum apiculatum* was the most abundant species within communal rangelands. Although *C. apiculatum* has a heavy wood ideal for fuelwood (Van Wyk 1990, Shackleton *et al.* 1998), it had been relatively little harvested. A likely explanation is its predominance in the drier eastern part of the study region where settlements are smaller and more isolated and woodland resources less intensively utilised. *T. sericea* and *D. cinerea*, in contrast, grow in higher densities in the moister western part of the study region, together with the largest settlements and associated greater demand for woodland resources. In protected areas, the only woody plant species to have been harvested to any perceptible extent were those with relatively hard (perhaps termite-resistant) wood, valuable as fire wood, lodge construction timber or fence poles for the reserve boundaries.

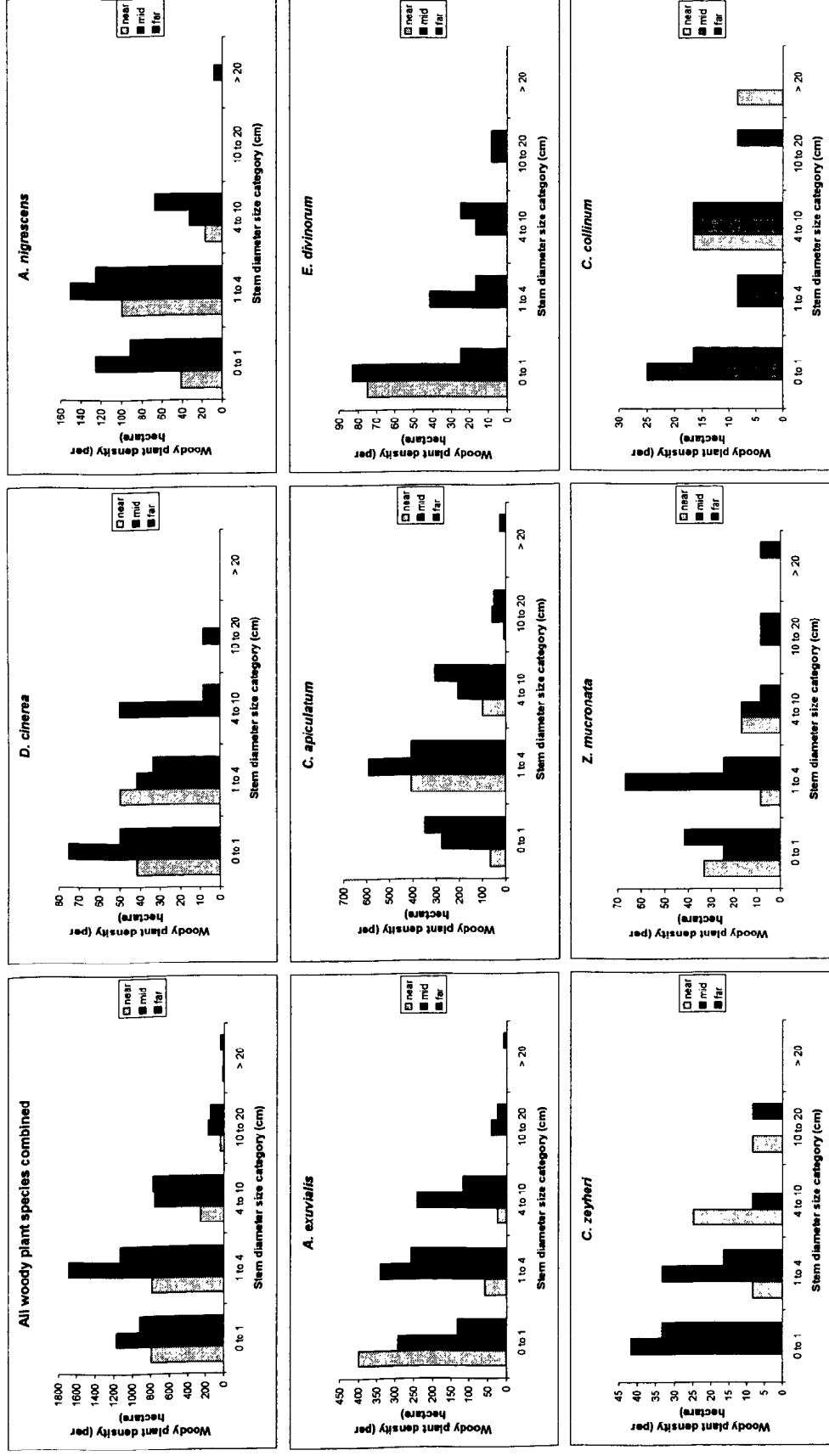


Figure 5. Contrasting stem diameter distributions representing population structure, for all woody plants combined and for common species, with distance from Thorndale settlement.

Live wood harvesting has considerably altered the population structure of the most frequently cut species within communal rangelands relative to protected areas. *T. sericea* plants between 10 and 20 cm in stem diameter, i.e. 'small reproductive woody plants', were at significantly lower densities in communal rangelands than in protected areas. Of those species heavily utilised, the harvesting of woody plants of an intermediate to large size has reduced the proportion of their populations considered to be reproductively mature and seed-producing, with obvious implications for future regenerative capacity. Certainly, the preferential harvesting of 'poles' (0 to < 4 cm in stem diameter) and 'small reproductive woody plants' will result in a bottleneck in future recruitment of reproductively mature individuals.

T. sericea, favoured for fuelwood, construction timber, carving and its medicinal properties (Shackleton 2001), was undoubtedly the species with the most detectable signs of impact to its population structure, and consequently to its demography. It frequently grows in dense relatively mono-specific stands along seeplines (Tinley 1992). Its accessibility, together with single straight stem and hard wood make it highly attractive. Despite it being a relatively vigorous resprouter following harvesting damage (Chapter 5), *T. sericea* densities within communal rangelands were lower than in protected areas and plants were considerably smaller in diameter. In contrast, the low frequency with which both *Strychnos madagascariensis* and *Sclerocarya birrea* had been harvested and the relatively high density of large mature plants within communal rangelands reflects their value for the edible fruit they bear. Traditionally, in the study region, as found elsewhere (Luoga *et al.* 2000a), *S. birrea* was considered 'sacred' and protected from harvesting. Evidence of recent harvesting reflects both the disintegration of previous means of resource control and a scarcity of easily accessible alternative wood resources.

Most savanna woody plants are able to resprout following damage of their aboveground parts, although the vigour with which they do so differs (Chapter 5). The majority of species favoured by harvesters were significantly more multi-stemmed within communal rangelands than in protected areas, this being

particularly pronounced for plants of an intermediate size. *T. sericea* provides a clear illustration of this, being consistently single-stemmed in protected areas with three or four stems per plant in communal rangelands. *Albizia harveyi*, however, showed little resprouting response and may be especially vulnerable to intensive harvesting, being slow-growing (Van Wyk 1990), highly favoured by harvesters and with a low density of newly recruited plants recorded in communal rangelands. The more branched growth forms of woody plants within communal rangelands appear to be frequently associated with a vegetative non-reproductive state.

For the majority of woody plant species, there were relatively fewer seedlings within communal rangelands than in protected areas. There does not, therefore, appear to be compensatory recruitment in response to woodland thinning. However, the most heavily utilised communal rangeland site provides an interesting anomaly. This site was in close proximity to the largest settlement in the study region and had been heavily thinned, with five of the species occurring in the adjacent protected area found to be absent. Relative to all other communal rangeland and protected area sites, the higher number of seedlings sampled at this site may reflect some threshold level of woodland thinning to be crossed before compensatory recruitment occurs, provided recruitment conditions are favourable. Alternatively, these small plants may have been predominantly root suckers, in response to intensive anthropogenic disturbance.

The density of woody plant recruits, particularly of species considered to be acceptable to browsers, was especially low in the vicinity of the settlement. It is here that goats concentrate their feeding activity. On the other hand, seedlings and small plants of a couple of species considered undesirable to browsers, *Euclea divinorum* and *Acacia exuvialis*, occurred at higher densities close to the settlement than further away. Activities associated with human settlements increase unfavourable recruitment conditions and reduce seedling recruitment. These conditions include soil compaction by livestock trampling; loss of grass cover; reduced plant available moisture; an altered nutrient status and a reduction in the number of large woody plants that produce seeds and shade young seedlings

from desiccation (Ererwijn & Verhoeven 1995, O'Connor 1995, Hoffman 1996, Rathogwa 1999).

Even with the exclusion of those woody plants that had been cut, plants growing in the vicinity of the settlement were significantly shorter and more multi-stemmed than those further away. Intensive browsing by livestock suppresses the height gain of woody plants, aggravating the effects of harvesting damage by consuming resprout shoots and limiting reproductive output (Ererwijn & Verhoeven 1995, Moss 1996). *T. sericea* and *D. cinerea*, dominant within the most heavily utilised communal rangeland site, were transformed by live wood harvesting/livestock browsing into multi-stemmed shrubs scarcely taller than the grass layer (Photograph on page 32. *Bottom left*). There was no suggestion of bush thickening in communal rangelands, as documented by other studies in response to severe grazing pressures (Prins & Van der Jeugd 1993, Rocques *et al.* 2001), with densities clearly suppressed by wood harvesting and livestock browsing.

Sampling the woodland along a gradient of decreasing disturbance intensity with distance from a settlement, revealed clear patterns that reaffirm the conclusions drawn at the larger scale of contrasting land uses. The study's findings complement those of Shackleton *et al.* (1994) and Ererwijn & Verhoeven (1995) from the same region and for other vegetation types (Skarpe 1990, Grundy *et al.* 1993, Luoga *et al.* 2002). These document disturbance-intensity related shifts in species dominance and population structure, including the loss of larger size classes, a subsequent reduced recruitment capacity and a lowered standing wood biomass. Similar vegetation trends have been observed in response to animal activity close to water points (Andrew 1988, Landsberg *et al.* 2002). Changes in the population structure of woody plants precede species compositional changes and are therefore useful indicators of utilisation impact and declining recruitment (Walker *et al.* 1986, Shackleton 1993).

In conclusion, live wood harvesting from woodlands within the communal rangelands of the Bushbuckridge study region has substantially impacted on the demography and regenerative capacity of the most heavily utilised woody plant species. Despite these species having the ability to resprout, current wood

harvesting within communal rangelands appears to be unsustainable, with a lowered standing wood biomass, densities of mature seed-producing woody plants considerably reduced and little evidence of compensatory recruitment. If not at present, localised shortages of fuelwood are imminent, with densities of suitably sized woody plants within the communal rangelands surrounding the largest settlements severely reduced. Smaller settlements within the eastern part of the region continue to have access to more abundant fuelwood supplies, including high densities of *C. apiculatum*. However, increasing numbers of external users are harvesting wood from these woodlands and in many cases selling it in other settlements where the fuelwood resource base has already collapsed (Twine 2002). Long-term woodland integrity and availability of fuelwood resources cannot be adequately ensured without the economic upliftment of those people whose livelihoods rely heavily on them. In the short term, however, actions that support the recovery of savanna woodlands are needed. These must be complemented by harvesting policies and programmes that fit within a holistic energy approach (Dovie *et al.* 2004). A sustainable harvesting approach could include measures such as: protecting newly recruited plants and plants recovering from previous harvesting; safeguarding the capacity of woody plant populations to continue recruiting through selective harvesting and monitoring; the controlled harvesting of alternative woody plant species; woodlots or planting programmes for fast-growing suitable fuelwood species; and allowing access to surplus wood on nearby private and state land. That live wood harvesting within the Bushbuckridge region has visibly altered the demography of the most abundant species, as well as those species previously considered ‘sacred’, should galvanise measures to pre-empt impending woodland degradation and a potential localised fuelwood crisis.

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CHAPTER 3

Woody Plant Allometry and Demography in a Semi-Arid African Savanna

Abstract

Many savanna woody plant species show a clear shift in growth strategy, from a sapling or ‘small plant’ phase characterised by height gain to a ‘large plant’ phase showing a reduced height relative to stem diameter increment. The height at which this change in allometric relationship occurs coincides with the height at which woody plants become less vulnerable to fire damage and are generally considered to become reproductive. For other species, the relationship between height and stem diameter was consistently linear across their entire size range. Saplings of the eleven study species did not differ radically in the slope of their height to stem diameter allometric relationships. However, certain patterns were evident: saplings of species with a high wood density had a proportionally larger height increment than those species with lighter wood, while saplings of species characterised as having a higher degree of branching had a higher aggregate stem diameter increment. Those species showing an obvious size-associated change in growth allocation had a relatively larger height increment during the sapling phase than those that did not. Of the study species, *Sclerocarya birrea* saplings differed the most noticeably in their growth strategy: focusing growth first into stem diameter increment and then into (probably rapid) height gain until above the ‘flame zone’. In general, population structures showed little evidence of episodic recruitment events and were substantially similar under both protected area and communal rangeland land use. Interpretations of population distributions are, however, highly influenced by ‘classic’ assumptions of constant growth across the entire size class range.

Keywords: growth form; growth strategy; land use; recruitment; population structure; size class distributions

3.1 INTRODUCTION

Woody plant architecture can be informative in identifying the relative importance of influential factors in different environments (Archibald & Bond 2003). Even within the same environment, different factors could favour vastly different growth forms. The growth form of a mature plant as the outcome of the environmental and genetic factors that have been operating throughout its lifetime, has substantial ecological implications: influencing light interception, stability against wind, defence against herbivores and fire, and the timing of reproduction (Kohyama & Hotta 1990, Coomes & Grubb 1998, Archibald & Bond 2003).

Much of current ecological theory regarding the adaptive significance of inter-specific tree architectural variation is based on empirical and simulation studies of temperate and tropical forest trees, where light is considered the most important limiting factor. Understanding how forest trees survive through the sapling stage and grow into adult trees is fundamental (Kohyama & Hotta 1990). Variation in the allometry of understorey saplings is held to reflect a species-specific trade-off between height growth for exploiting opportunities to reach better-lit conditions while delaying reproduction and horizontal growth for effective light assimilation and reproduction in the present. The shape of saplings reflects whether they are gap specialists that prioritise height gain, or shade tolerant, emphasising lateral spread.

But what of woody plants growing in conditions where light is not limiting? Is it possible to similarly interpret their inter-specific allometric variation as alternative survival strategies in response to influential factors other than light? Trees in savannas and more arid environments are often widely scattered and instead of light being of paramount importance, fire and browsers are expected to strongly influence woody plant growth form (Archibald & Bond 2003). Do the saplings of savanna woody plant species, growing within the same region and exposed to the same set of influential factors, differ in their allocation of growth to height versus lateral spread to increase the likelihood of survival and success within their environment? A fire can destroy, or ‘topkill’, the entire aboveground biomass of a

woody plant. Woody plants below 3 m in height have a high probability of topkill, whilst those that are taller suffer only minor shoot damage (Trollope 1984). Growth invested principally in height gain bears the cost of delayed reproduction and therefore the benefits of height gain depend on the “pervasiveness of destructive agents” (Falster & Westoby 2003). Do some savanna woody plant species channel growth first into height gain to ‘escape the flame [or browse] zone’ (Higgins *et al.* 2000) and only then reproduce? Alternatively, others may develop greater defense: thicker bark (Wilson & Witkowski 2003), spines or high leaf tannin content (Owen-Smith & Cooper 1987), making them less vulnerable to damage and able to reproduce opportunistically as they grow through this zone of frequent disturbance. Is interspecific variation in resource allocation to wood density associated with different growth strategies? Enquist *et al.* (1999) found that for tropical dry forest species there was essentially a trade-off in growth rate with allocation to tissue density: species that allocate less biomass to their stems (light woods) increase in basal diameter faster than species that allocate more (dense woods).

Theories regarding the factors influencing woody plant demography and the means for characterising population structure are similarly founded to a large extent on empirical studies of forest species (Condit *et al.* 1998, Coomes *et al.* 2003, Niklas *et al.* 2003). The size class distribution of a woody plant species describes its population structure at a point in time. It results, however, from the dynamic processes of stem recruitment, growth and mortality. Recruitment adds new plants to the smallest size class, a size-specific growth process determines the rate at which plants move through size classes and size-specific mortality determines the number that die (Coomes *et al.* 2003). For forest species, a recruiting population is classically represented by a continuous monotonically declining curve, showing recruitment of new individuals, growth through size classes, a constant rate of attrition and sufficient mature individuals for continued recruitment. Yet, demographic studies show that most forests have an age-structure reflecting past disturbances and there are probably no forests that have achieved a balanced age distribution (Harper 1977). Coomes *et al.* (2003), using large data sets of forest species, determined that a single function could not

effectively describe population structure across the entire size class range. Instead, scaling functions provided the best fit to smaller stems, while negative exponential functions (an inverse-J shape) more accurately represented larger stems. These patterns are consistent with competition for a limiting resource (e.g. light) shaping the small-stem phase, with the smallest trees having the highest probability of mortality (Enquist *et al.* 1998) and exogenous disturbance (e.g. windfall) shaping the large-stem phase, with disturbances likely to kill trees regardless of their size and resulting in mortality in a given size class that is proportional to the number of trees in that size class.

Even though the influential factors differ, do the population structures of savanna woody plants show similar patterns, with seedlings having a substantially higher mortality rate than larger plants and with plants of all sizes affected by exogenous disturbances, with the rate of mortality in a given size class proportional to the number of stems in that size class? Or do population structures indicate that with increasing size, savanna woody plants have an enhanced resistance to fire, browsers and drought? Do the size frequency distributions of savanna trees differ from those of regularly recruiting forest trees by showing evidence of episodic recruitment in response to variable rainfall, or of irregular bursts of growth through size classes in response to a temporary release from suppressing factors such as fire, herbivory or water limitation? In arid savannas, seedling recruitment of many woody plant species is limited to years of above-average rainfall. On the other hand, recruitment in mesic savannas is more likely to be suppressed by frequent fires and competition with grasses for light and water (Scholes 1997, Jeltsch *et al.* 1998, Higgins *et al.* 2000).

By comparing the growth forms and population structures of eleven common woody plant species within a semi-arid savanna woodland region, across two different land uses, the primary aim of this study was to identify whether syntopic species show differences that can be interpreted as alternative growth and recruitment strategies. More specifically, the study aimed to determine whether:

1. Species formed distinct groupings according to similarities in ‘tree architecture’, with groups differing in: (i) the allometric relationship

between plant height and basal stem diameter and (ii) species-specific characteristics of wood density, stem number per plant and the maximum height attained.

2. Groups indicate growth patterns or strategies, distinguishing between: (i) species that initially focus growth into height gain until a threshold ‘less vulnerable’ height is reached, following which resources are allocated to alternative processes, e.g. reproduction (Archibald & Bond 2003; Wilson & Witkowski 2003) or belowground biomass storage, and (ii) those species that remain longer, and possibly reproduce, within the ‘flame zone’ (Gignoux *et al.* 1997, Maze 2001).
3. The population size frequency distributions of savanna woody plant species deviate from the classic monotonically declining curves representing ‘healthy’ continuously recruiting natural forest populations, instead showing evidence of pulsed recruitment and sporadic growth in response to episodically favourable conditions.

3.2 METHODS

3.2.1 Study area and approach

The study region was located within the Bushbuckridge area (centring on 31° 17' E; 24° 39' S) of the South African ‘lowveld’ of the Limpopo Province. The area was delimited by Acornhoek settlement in the west and Manyeleti Reserve bordering the Kruger National Park in the east (refer to Chapter 2 for a map of the study region, and details of land use and biophysical characteristics). Within this region, five sites were located in woodland areas of the communal rangelands surrounding the settlements of Acornhoek, Welperdiend, Gottenberg, Utlha and Phungwe and each was paired with a site located less than 2 km away, in the woodlands of adjacent protected areas - Wits Rural Facility, Timbavati, Manyeleti (two sites) and the Sabie Sand Game Reserve, respectively. The vegetation of the region is broadly classified as Mixed Lowveld Bushveld (Van Rooyen & Bredenkamp 1996). All study sites were located within broad-leaved

savanna woodlands on the relatively level ground of upland areas. Eleven study species were selected to represent a range of woody plant growth forms.

3.2.2 Field data collection

At each site, data were collected along eight 100 m long transects comprising two sampling widths: 4 m wide for woody plants less than or equal to 4.5 m in height and 40 m wide for those more than 4.5 m in height, these being far fewer. Transects were positioned: (i) with the long axis along a north-south compass bearing, (ii) for communal rangelands, in woodlands that had not been cleared for agricultural fields, appearing ‘relatively intact’ to the eye and (iii) for both communal rangeland and protected areas, as systematically and equidistantly as possible within the wooded area.

The information recorded for the selected species included: species, plant height (height of the tallest live stem) and basal stem diameter (measured close to the ground or just above the basal swelling when present). For multi-stemmed plants, the number of stems growing from the plant base was recorded and the diameters of all stems were measured.

3.2.3 Data Analysis

All analyses were at the plant level. For multi-stemmed plants, total stem diameter was determined by calculating the cross-sectional areas of all composite stems, summing them and using this aggregate stem area to calculate the effective total stem diameter. Only intact woody plants were used in the analyses, i.e. plants with evidence of cutting or substantial breakages were excluded since allometry (height to diameter relationship) and resource allocation to growth and reproduction are likely to have been affected. Total densities of all woody plants at each site were not determined, with species other than those selected for the study having a minimal presence and therefore assumed to have little influence on the population dynamics of the study species.

3.2.3.1 *Woody Plant Allometry*

Both woody plant height and total stem diameter data were $\log_{10}$ transformed to reflect the proportional growth increment of height to stem diameter. A regression function of the relationship between height and stem diameter dimensions was calculated for each species. Although regression analyses found differences in woody plant height:diameter allometry associated with land use for certain species, samples sizes were large and differences proved biologically insignificant (Appendix 4). Even for the most abundant and heavily utilised species, *Terminalia sericea* and *Dichrostachys cinerea* (Chapter 2), differences amounted to only a few (< 5) centimetres in height. The data from both land uses were therefore pooled.

For several species, the proportional gain in height to diameter appeared substantially different for small and large sized plants. For these species segmented (or piecewise) regressions were fitted, in which the relationship between height and diameter followed a linear regression up to a break point after which the slope of the trend line changed significantly (Piepho & Ogutu 2003). Break points were determined from indexed plots of the deviances (Figure 1 on page 68) (Crawley 2002). One of the assumptions of regression analysis is that measurements of the explanatory (X) variable are obtained without error. In practice this is often impossible, although by assuming that the errors in X data are negligible or at least small compared with the measurement errors in the dependent (Y) variable (which holds true here), regression statistics are sufficiently robust to cope with violation of this underlying assumption (Zar 1996, Quinn & Keough 2002).

The architecture of woody plant saplings changes with ontogeny and by fitting allometric relationships these changes in morphology can be examined from a dynamic perspective (King 1990), enabling an understanding of how trees survive

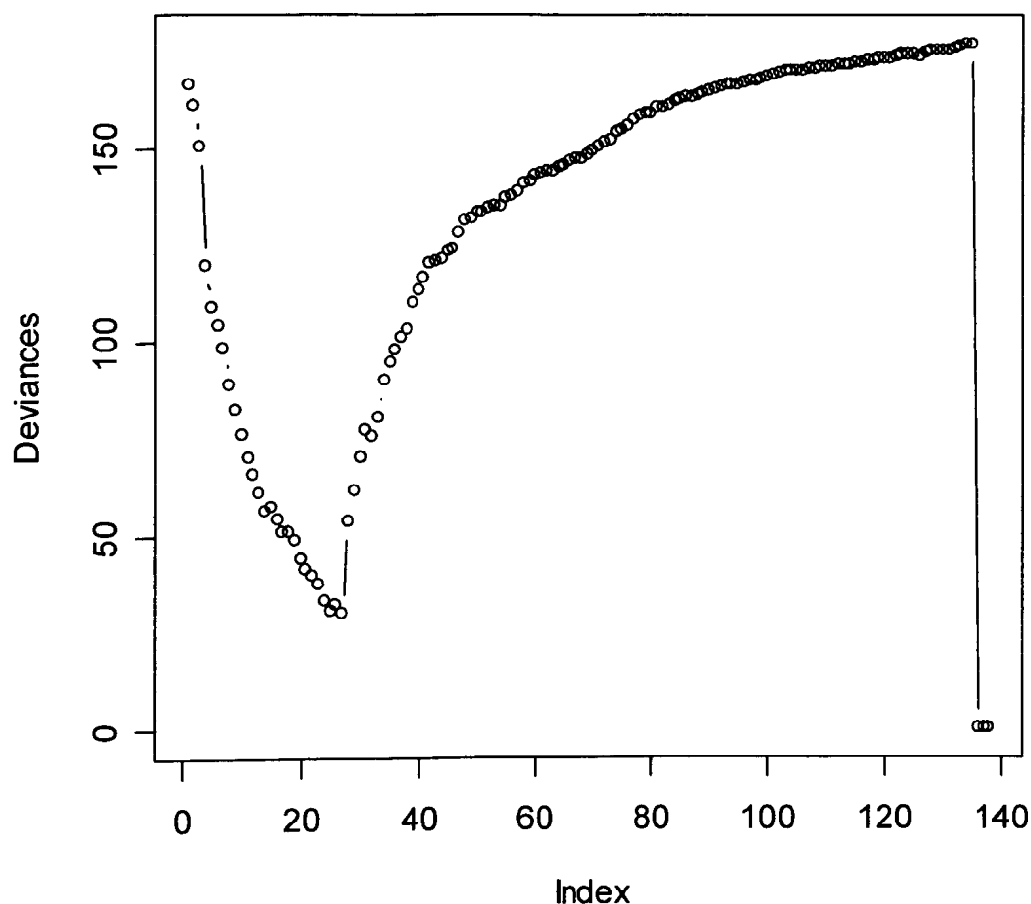


Figure 1. An example of a plot of deviances in an indexed series (species represented: *Sclerocarya birrea*) showing a sharp U-shape as the fit gets progressively stronger up to a certain index value (27 in this case - corresponding to a stem diameter of 4.6 cm), then progressively weaker as the break point is placed too far to the right.

through the sapling stage to grow into adults. Species can then be compared by estimating the parameters b_0 and b_1 in allometric equations of the form:

$$\log y = b_0 + b_1 \log x,$$

where x and y are dimensions of the plant, in this case stem diameter and height respectively. To compare the height to diameter relationship across species for the small plant or sapling phase, the previously determined linear regression functions (the small plant phase for species for which segmented regressions had been fitted and the single regression function for the remaining species) were plotted together. Slopes and elevations were compared using standard ANCOVA tests.

Subsequently, a post-hoc Tukey test with unequal sample sizes was carried out (Zar 1996), consistent with the original hypothesis tested, to identify groupings of species with similar height:diameter growth allocation patterns. Interpretations were made taking into account species-specific characteristics, i.e. mean wood density, maximum height attained and stem number per plant (Table 1 on page 70). Maximum height values were calculated as the mean height of the ten tallest trees sampled for each species. Wood density values (a measure of the total dry mass per unit volume of wood (kg m^{-3})) were taken from the literature (Van Wyk 1990).

3.2.3.2 Population Structure and Recruitment Patterns

Woody plant population structure has generally been represented as a histogram of stem diameters and statistically described in terms of the regression curve that best approximates the change in the number of woody plants in successive stem diameter size classes (Niklas *et al.* 2003), or by using a number of other descriptive indices (Wiegand *et al.* 2000). Data from all protected area sites and all communal rangeland sites were pooled to construct ‘protected’ and ‘communal’ stem diameter frequency distributions for each species. In determining the number of woody plants represented by each size class, account was taken of the two-width plot design with the number of woody plants ≤ 4.5 m in height adjusted according to the area sampled for larger plants. For statistical purposes a uniform bin- (or interval) size (Δx) is required to sort individuals into different size classes. A Δx of 4 cm was chosen to limit the number of size classes with only a few individuals. Comparison of size class distributions with a smaller size class interval ($\Delta x = 2$ cm) found no visible difference in the information contained. Height size frequency distributions were similarly constructed for each species for both protected areas and communal rangelands, using 1 m height size class intervals. The size frequency distributions of each species, for both land uses, were compared using Kolmogorov-Smirnov distribution tests.

Table 1. Details of the study species, including description of growth form (Van Wyk 1990); mean maximum height in study area (max. Ht); mean stem number per plant $\pm$ SD; stem number range (min-max); wood density (values from Van Wyk 1990). Species nomenclature according to conventions used in Germishuizen & Meyer (2003).

Species	Family	Growth Form	max. Ht (m)	mean Stem No.	Stem no.	Wood Density (kg m ⁻³)
<i>Albizia harveyi</i> E. Fourn.	Fabaceae	s/ms m tree	8.6	2.1 $\pm$ 1.7	1 - 6	800
<i>Combretum apiculatum</i> Sond.	Combretaceae	s/ms m tree	9.5	2.0 $\pm$ 1.8	1 - 6	1230
<i>Combretum collinum</i> Fresen.	Combretaceae	s/ms m tree	9.4	3.2 $\pm$ 2.9	1 - 13	960
<i>Combretum zeyheri</i> Sond.	Combretaceae	s/ms m tree	7.1	4.8 $\pm$ 3.1	1 - 18	750
<i>Dalbergia melanoxylon</i> Guill. & Perr.	Fabaceae	s/ms m tree	6.3	1.7 $\pm$ 1.3	1 - 6	1280
<i>Dichrostachys cinerea</i> (L.) Wight & Arn.	Mimosoideae	ms s tree	6.1	2.4 $\pm$ 1.9	1 - 10	960
<i>Lonchocarpus capassa</i> Rolfe	Fabaceae	ss m tree	9.0	1.8 $\pm$ 1.3	1 - 6	770
<i>Sclerocarya birrea</i> (A. Rich.) Hochst.	Anacardiaceae	ss b tree	12.4	1.1 $\pm$ 0.5	1 - 2	560
<i>Stychnos madagascariensis</i> Poir.	Loganiaceae	ms m tree	7.4	3.6 $\pm$ 2.7	1 - 13	850
<i>Terminalia sericea</i> Burch. ex DC.	Combretaceae	ss m tree	8.0	1.7 $\pm$ 1.4	1 - 6	880
<i>Ziziphus mucronata</i> Willd.	Rhamnaceae	ss m tree	9.1	1.7 $\pm$ 1.2	1 - 7	880

Abbreviations

Growth Form

ms - multi-stemmed

ss - single-stemmed

s - small

m - medium

b - big

A combination of methods was used to describe the population structures of the study species and to contrast their patterns of recruitment and the influence of exogenous disturbance. Firstly, following the methods of Condit *et al.* (1998), Lykke (1998) and Obiri *et al.* (2001), a least-squares linear regression was calculated to describe the slope of the stem diameter size frequency distribution for each species and each land use. The size frequency distribution slopes were interpreted following Everard *et al.* (1994) with species defined according to their observed regenerative capacity: a negative slope typically indicating a population with ongoing recruitment (or growth suppression); a more horizontal slope indicative of a population composed of a relatively uniform number of individuals across all size classes and showing either little recruitment or a relatively high number of large plants (perhaps from previous recruitment episodes); and a positive slope reflecting a population with little recent recruitment but possibly episodic recruitment in the past (or perhaps accelerated growth across intermediate size classes). Secondly, quotients, calculated between successive size classes, provide a measure of a population's constancy (Harper 1977) being a measure of growth from one size class to the next. In a 'stable' population, the quotient between the numbers of trees in successive size classes approaches a constant value, with the assumption of constant growth across size classes. Further analysis of the size class distributions was carried out following methods used by Coomes *et al.* (2003) (Appendix 5).

Irregular size distributions are not adequately described by commonly used indices, as they fail to describe the deviation from a monotonically-declining shape (Wiegand *et al.* 2000). Additional characterisation of species population dynamics was therefore made using Simpson's Index of Dominance (C) and a Permutation Index (P) developed by Wiegand *et al.* (2000). The combination of the Simpson's and Wiegand *et al.*'s (2000) Permutation indices is considered effective in describing size frequency distributions that deviate from 'ideal' regularly-recruiting populations and which are shaped by rare recruitment events and irregular growth. Simpson's Index of Dominance (C) measures the occurrence

of dominant size classes or the evenness of occupation of size classes (Wiegand *et al.* 2000):

$$C = 1/(N(N-1)) \sum_{i=1}^n N_i(N_i - 1),$$

where N is the total number of woody plants and N_i the number of woody plants in class i ; n is the number of size classes. For *Acacia raddiana* occurring in the arid Negev desert, Wiegand *et al.* (2000) interpreted Simpson's index values greater than 0.1 to reveal a size frequency distribution that is steeper than expected from an exponentially-declining population, a consequence of rare recruitment events and irregular growth due to episodic rainfall. Simpson's values below 0.1 represented more evenly distributed size classes.

Wiegand *et al.*'s (2000) Permutation Index (P) measures deviation from a monotonically declining size distribution expected for an 'ideal' recruiting population. For such a population, ranking would be equivalent to enumerating the size classes from the class representing the smallest (most frequent) to that representing the biggest (least frequent) trees. The absolute distance between the expected and the real location (rank) of all the size classes are summed, ignoring the relative frequencies of the different size classes. If a size distribution is discontinuous, with larger individuals in preceding size classes, the Permutation Index (P) is higher than that of a continuous monotonically declining population:

$$P = \sum_{i=1}^n |J_i - i|; \quad J_i = 1 \text{ to } n,$$

where J_i is the rank of size class i ($i = 1$ for the smallest woody plants), with the highest rank ($J_i = 1$) given to the most frequent size class; n is the number of size classes.

R freeware (version 1.7.1.) and STATISTICA (version 5) software were used for statistical analyses.

3.3 RESULTS

3.3.1 Woody Plant Allometry

For five species, *Albizia harveyi*, *Combretum collinum*, *Combretum zeyheri*, *Lonchocarpus capassa* and *Strychnos madagascariensis*, a reasonably consistent linear allometric relationship between woody plant height and stem diameter pertained across the entire stem diameter range (Table 2 on page 74, Figure 2 on pages 75-76). In contrast, the relationship between height and stem diameter for the six remaining species, was significantly different for small and large plants, with a lower height increment relative to diameter increment shown by larger plants. Segmented regression analyses determined this change in growth allocation to occur, for all species, at a height of approximately 3 m and a stem diameter of roughly 10 cm. *Sclerocarya birrea* had a notable absence of intermediate-sized plants, i.e. 4.7 to 11.0 cm in stem diameter and 2 to 4 m in height.

The allometric relationship between woody plant height and stem diameter for the small plant or sapling growth phase of each species was compared. The contrast involved either the single regression function fitted to this relationship or for those species where segmented regression functions had been more appropriate, the regression function fitted to the data range falling below the break point (Figure 3 on page 77). ANCOVA test results indicated that regression slopes differed significantly between species ($F_{0.05(1),2,2878} = 207.7$, $P < 0.05$). However, post-hoc comparison tests yielded ambiguous results in the form of conclusions of overlapping sets of similarities (Zar 1996). Therefore, instead of distinct groupings of species according to differences in their relative growth allocation to height and stem diameter increment during the small plant phase, there appears to be a gradation, with some species investing slightly more growth into height gain. Nevertheless, two broad groupings of species were discernable, differing in regression height intercepts, and of interest for the characteristics common to the species they contained (Group 1: $\log_{10}(\text{height})$ intercept = -0.219 ± 0.01 (SE); Group 2: $\log_{10}(\text{height})$ intercept = -0.257 ± 0.006 (SE); paired t-test statistic = 2.42; $P < 0.05$; d.f. = 10). The first group contained seven species, the uppermost

six (*Terminalia sericea*; *Combretum apiculatum*; *Dichrostachys cinerea*; *Dalbergia melanoxylon*; *Ziziphus mucronata* and *C. collinum*) having the highest wood density of the study species. Of the species comprising this group, only *C. collinum* and *C. zeyheri* had not shown a change in growth allocation associated with plant size. Both are multi-stemmed plants that grow proportionally more in aggregate stem diameter than in height during this sapling phase. With the exception of *S. birrea*, a single linear relationship between height and stem diameter represented the allometry of the species comprising the second group for their entire sampled plant size range. *S. birrea* was the shortest at any particular stem diameter during this sapling phase, despite it being the species that attains the tallest maximum height. *L. capassa* and *A. harveyi* also invested relatively more resources into diameter increment than height during this small plant phase. *S. madagascariensis* had a larger height increment relative to stem diameter than the other species in the group.

Table 2. Regression equations of the allometric relationship (log-log) between stem diameter (cm) and height (m) for each of the study species. For several species a segmented regression was fitted to the small and large plant phases; the *break point for segmented regressions was determined from an indexed plot of the deviances.

species	regression break point*	intercept $\pm$ SE	slope $\pm$ SE	R ²
<i>A. harveyi</i>	-	-0.255 $\pm$ 0.018	0.714 $\pm$ 0.034	0.78
<i>C. collinum</i>	-	-0.133 $\pm$ 0.024	0.699 $\pm$ 0.023	0.92
<i>C. zeyheri</i>	-	-0.136 $\pm$ 0.012	0.668 $\pm$ 0.012	0.87
<i>L. capassa</i>	-	-0.263 $\pm$ 0.029	0.728 $\pm$ 0.028	0.91
<i>S. madagascariensis</i>	-	-0.384 $\pm$ 0.009	0.889 $\pm$ 0.024	0.68
<i>C. apiculatum</i>	small phase ($\leq$ 5.3 cm)	-0.168 $\pm$ 0.008	0.847 $\pm$ 0.025	0.74
	large phase ($>$ 5.3 cm)	0.362 $\pm$ 0.022	0.315 $\pm$ 0.017	0.45
<i>D. cinerea</i>	small phase ($\leq$ 8.59 cm)	-0.194 $\pm$ 0.013	0.854 $\pm$ 0.025	0.70
	large phase ($>$ 8.59 cm)	0.335 $\pm$ 0.058	0.27 $\pm$ 0.052	0.11
<i>D. melanoxylon</i>	small phase ($\leq$ 7.5 cm)	-0.229 $\pm$ 0.015	0.877 $\pm$ 0.034	0.82
	large phase ($>$ 9.8 cm)	0.440 $\pm$ 0.146	0.213 $\pm$ 0.109	0.12
<i>S. birrea</i>	small phase ($\leq$ 4.6 cm)	-0.346 $\pm$ 0.036	0.755 $\pm$ 0.087	0.67
	large phase ($>$ 11.1 cm)	0.224 $\pm$ 0.05	0.403 $\pm$ 0.033	0.46
<i>T. sericea</i>	small phase ($\leq$ 7.6 cm)	-0.159 $\pm$ 0.009	0.883 $\pm$ 0.016	0.87
	large phase ($>$ 7.6 cm)	0.506 $\pm$ 0.025	0.201 $\pm$ 0.021	0.12
<i>Z. mucronata</i>	small phase ($\leq$ 5.3 cm)	-0.277 $\pm$ 0.057	0.911 $\pm$ 0.151	0.67
	large phase ($>$ 6.1 cm)	0.451 $\pm$ 0.048	0.228 $\pm$ 0.041	0.27

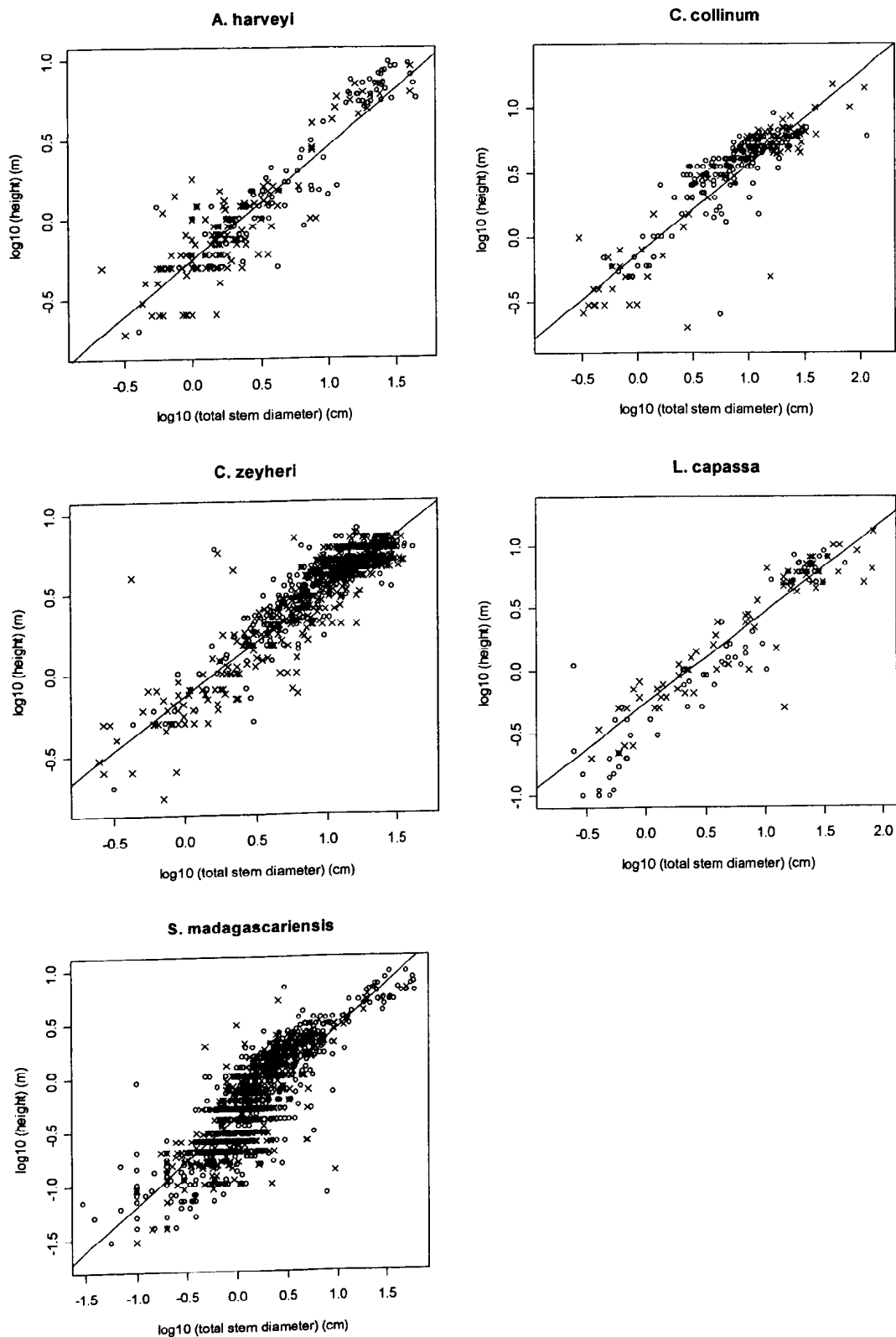


Figure 2. Relationship between woody plant height (m) and basal stem diameter (cm) (both $\log_{10}$ transformed) for each of the study species. Data from communal rangelands are represented by crosses.

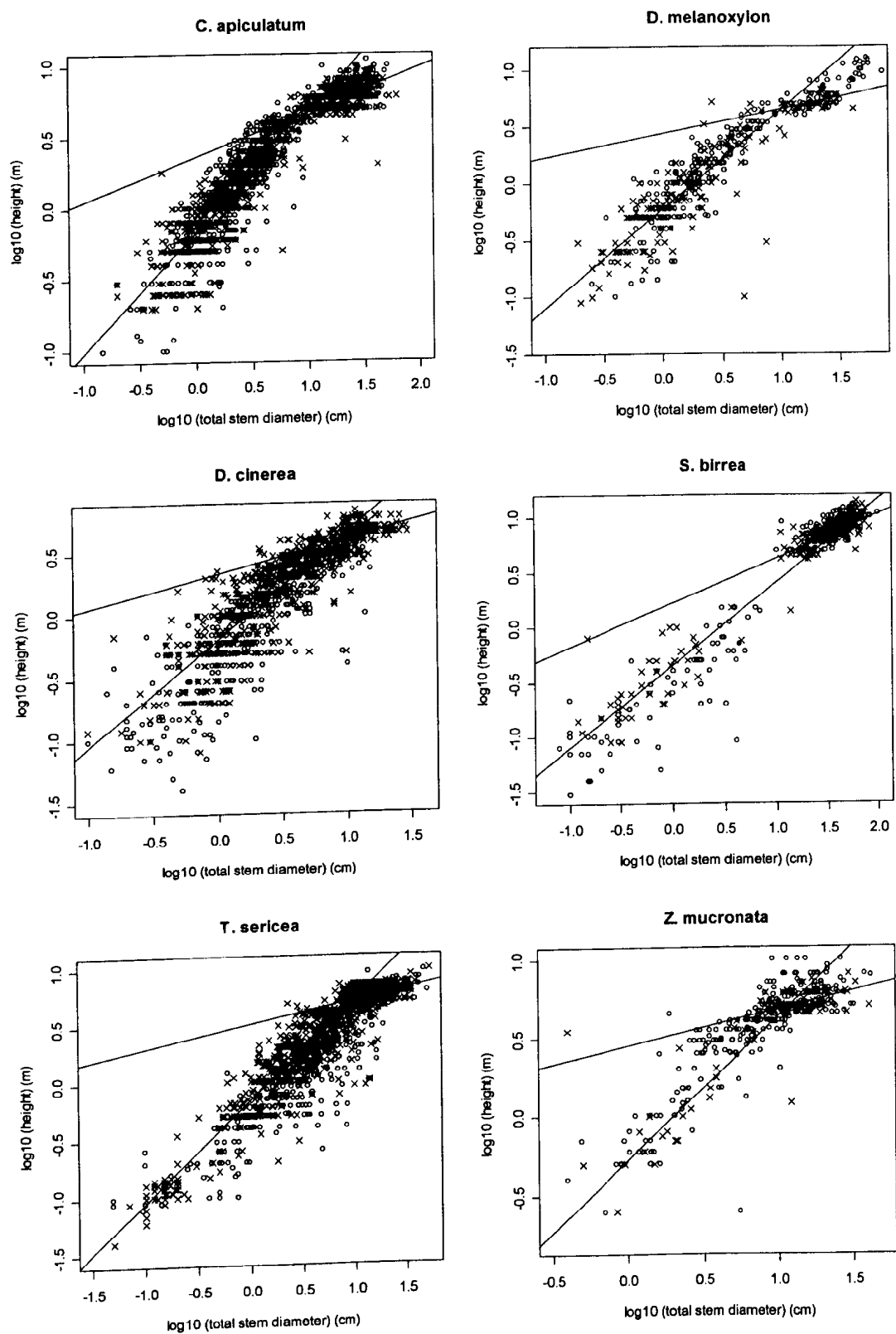


Figure 2 (continued). Relationship between woody plant height (m) and basal stem diameter (cm) (both $\log_{10}$ transformed) for each of the study species. Data from communal rangelands are represented by crosses. A segmented regression was fitted to the small and large plant phases.

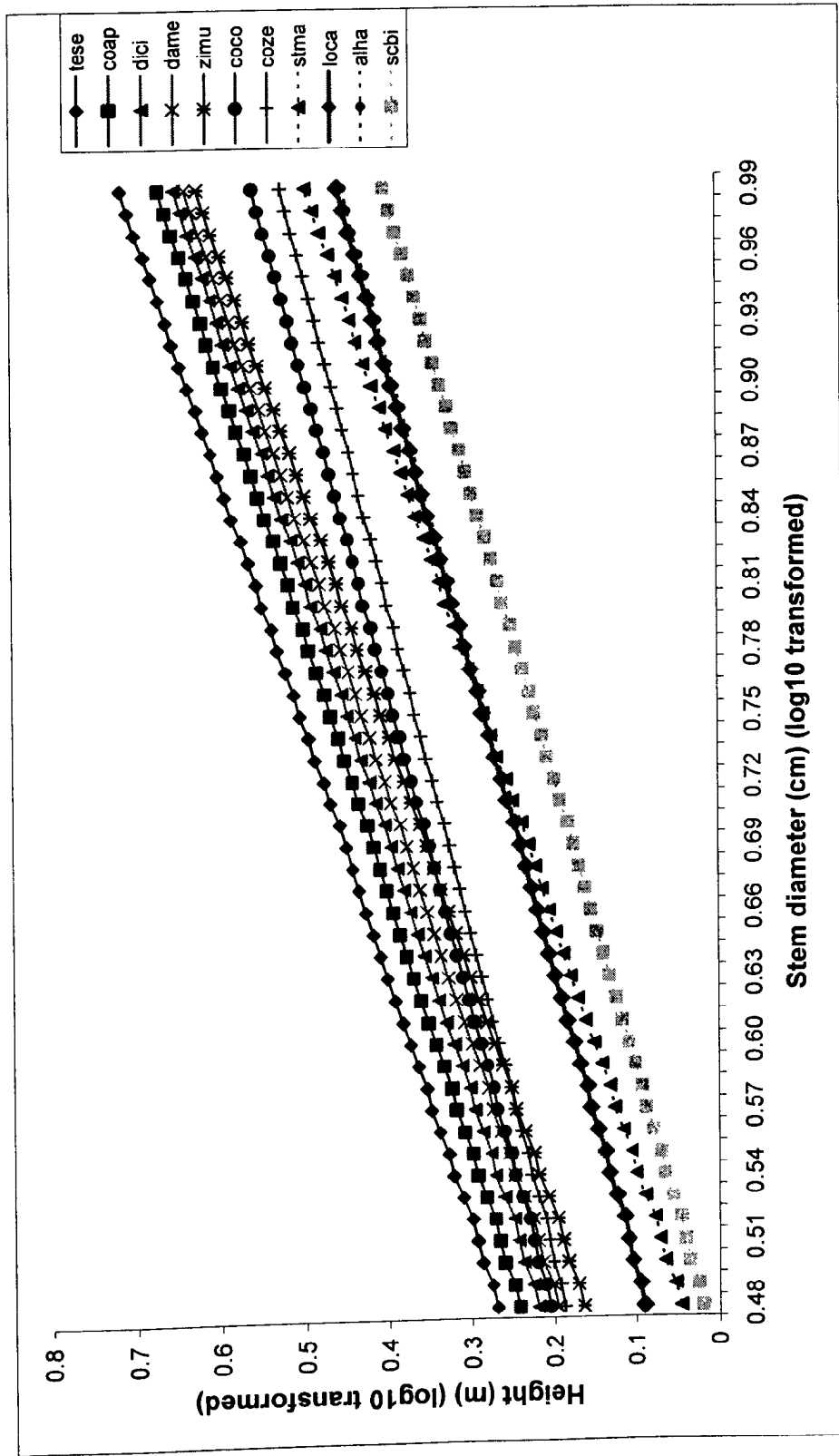


Figure 3. Predicted relationships between woody plant height and stem diameter (both log₁₀ transformed), for the saplings of the eleven woody plant study species.

3.3.1.1 Population Structure and Recruitment Patterns

Population structure was represented for each species, for both protected areas and communal rangelands, with stem diameter (Figure 4 on pages 79-80) and height size class distributions (Figure 5 on page 81, Appendix 6). Referring to the stem diameter size class distributions, most species had population structures that showed a relatively consistent attenuation of numbers from one size class to the next. However, there were discontinuities. For several species there appears to be a larger drop in numbers from preceding size classes, for woody plants of between 8 and 16 cm in stem diameter size, than expected under a constant attrition rate. Small *Z. mucronata*, *C. collinum* and *C. zeyheri* plants showed little reduction in number from the 0 to 4 cm diameter size class to the 4 to 8 cm diameter size class. *S. birrea*, the species with the most discontinuous population structure, appears to have a relatively humped population distribution, with a higher representation of plants of intermediate size (ca. 20 to 52 cm) than those of the preceding size classes containing plants 4 to 20 cm in stem diameter. Interestingly, *S. birrea* showed a lack of individuals sized 2 to 4 m in height under both land uses (as observed in the plot of height to stem diameter). The stem diameter frequency distribution showed few plants of size 8 to < 20 cm in stem diameter, especially within communal rangelands. Across all species, population structure appeared by and large consistent under either land use and Kolmogorov-Smirnov tests did not detect significant differences in either stem diameter or height size class distributions.

Woody plant species population structures were additionally characterised using population description indices (Table 3 on page 82) and plots of quotients (Figure 6 on page 83). Size class distribution slopes identified *D. cinerea* as being an abundant species with high seedling establishment and vigorous resprouting ability. On the opposite side of the continuum, *S. birrea*, was defined as having large mature trees, poor seedling establishment and little resprouting ability. Remaining species had size class distribution slopes with intermediate values,

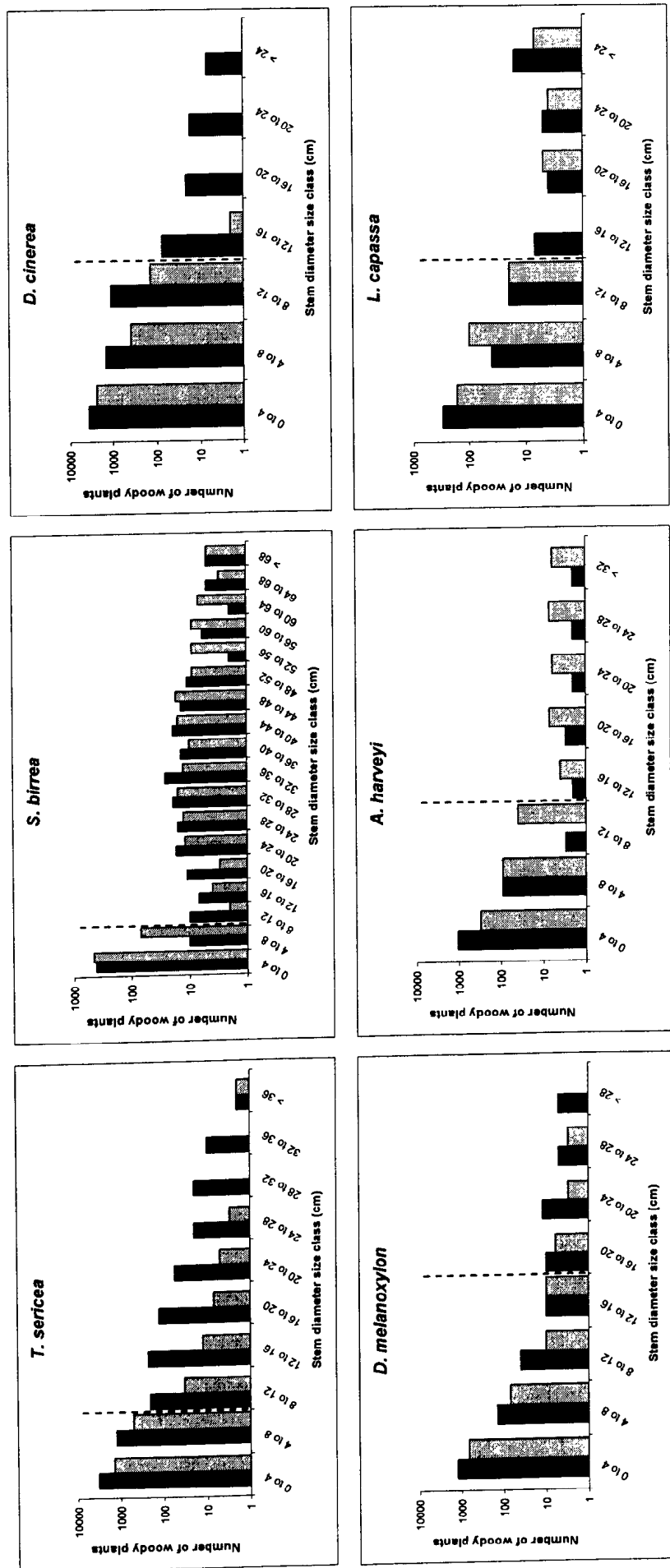


Figure 4. Population size frequency distributions for each study species within protected areas and adjacent communal rangelands. Black bars represent protected areas; Grey bars represent communal rangelands. The number of small plants (≤ 4.5 m in height) was adjusted ($\times 10$) according to the area sampled for taller plants (≥ 4.5 m); the vertical dashed line divides the adjusted from non-adjusted numbers of woody plants. The last size class represents the pooled number of large plants contained in subsequent size classes with fewer than five individuals.

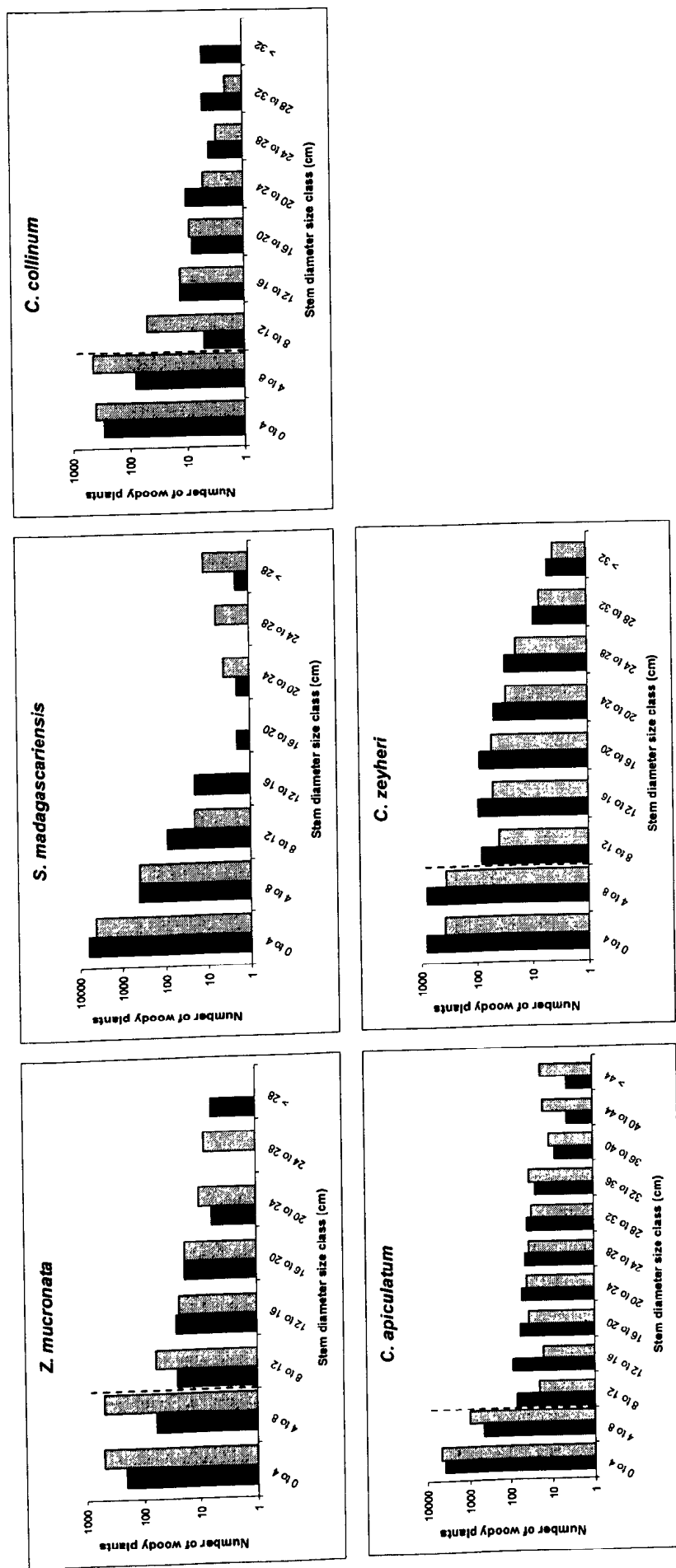


Figure 4 (continued). Population size frequency distributions for each study species within protected areas and adjacent communal rangelands. Black bars represent protected areas; Grey bars represent communal rangelands. The number of small plants (≤ 4.5 m in height) was adjusted ($\times 10$) according to the area sampled for taller plants (≥ 4.5 m); the vertical dashed line divides the adjusted from non-adjusted numbers of woody plants. The last size class represents the pooled number of large plants contained in subsequent size classes with fewer than five individuals.

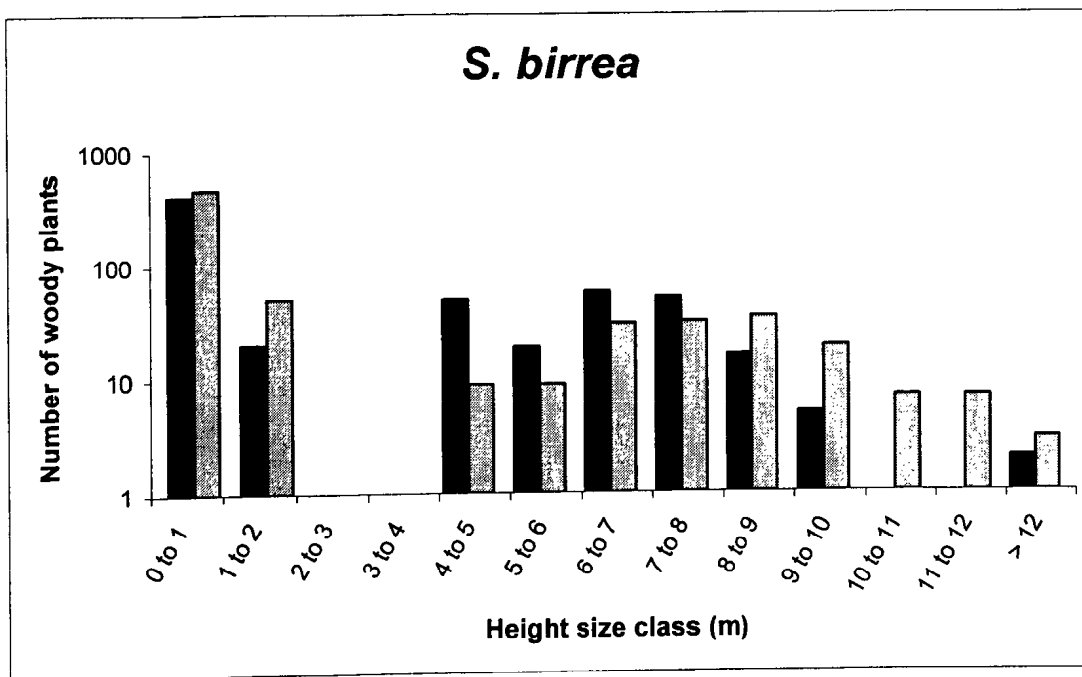


Figure 5. Woody plant height distribution of *Sclerocarya birrea* within protected areas and adjacent communal rangelands. Black bars represent protected areas; Grey bars represent communal rangelands.

indicating populations that were not declining, varying in the degree of seedling establishment and resprouting vigour. All species had relatively high (> 0.1) Simpson index values, reflecting uneven population distributions that, according to Wiegand *et al.* (2000), are steeper than expected for monotonically declining populations, i.e. showing a higher rate of attrition between successive size classes than expected for a regularly recruiting population with constant growth between size classes. *C. zeyheri* and *Z. mucronata* had the lowest Simpson's indices and therefore the most 'even' distributions, while *S. madagascariensis* had the highest and most 'uneven'. *S. birrea*, in both communal rangelands and protected areas and *C. apiculatum*, in communal rangelands, had relatively high Permutation indices indicative of more 'discontinuous' populations. *Z. mucronata*, *D. cinerea* and *T. sericea* had the most 'continuous' population size distributions.

Quotient plots reflected that the populations of all the study species fluctuated, under either land use, with many species, most notably *C. zeyheri*, showing

Table 3. Measures of population size structure for each of the study species within both protected areas and communal rangelands.

Species	Size Class Distribution (SCD) slope $\pm$ se*		SIMPSON's Permutation Index (C)		SIMPSON's Permutation Index (C)		SCD Slope Grouping **
	protected	communal	protected	communal	protected	communal	
A. harveyi	-0.23 $\pm$ 0.06	-0.16 $\pm$ 0.04	0.8	0.5	5	6	3
C. apiculatum	-0.12 $\pm$ 0.02	-0.10 $\pm$ 0.03	0.7	0.7	2	22	2or3
C. collinum	-0.13 $\pm$ 0.01	-0.14 $\pm$ 0.01	0.5	0.4	9	2	2or3
C. zeyheri	-0.14 $\pm$ 0.02	-0.13 $\pm$ 0.02	0.3	0.3	4	4	2or3
D. cinerea	-0.30 $\pm$ 0.04	-0.43 $\pm$ 0.06	0.4	0.7	1	2	4
D. melanoxylon	-0.20 $\pm$ 0.04	-0.19 $\pm$ 0.04	0.7	0.8	4	2	3
L. capassa	-0.19 $\pm$ 0.04	-0.20 $\pm$ 0.06	0.7	0.4	2	4	3
S. birrea	-0.03 $\pm$ 0.01	-0.02 $\pm$ 0.01	0.5	0.5	69	73	1
S. madagascariensis	-0.12 $\pm$ 0.03	-0.27 $\pm$ 0.10	0.9	0.8	1	8	3
T. sericea	-0.17 $\pm$ 0.02	-0.22 $\pm$ 0.03	0.5	0.6	3	1	3
Z. mucronata	-0.18 $\pm$ 0.03	-0.18 $\pm$ 0.03	0.4	0.4	2	0	3

* After Condit *et al.* (1998), Lykke (1998)

** SCD Slope Groupings (Everard *et al.* 1995)

1 - slope: approaching 0, poor seedling establishment; little resprouting ability; large mature trees

2 - slope: 0.04 - 0.1, saplings and seedlings at low densities but more than in group 1; some resprouting but declining pop's (often limited use as soft woods)

3 - slope: 0.1 - 0.2, vigorous resprouters; greatly used; populations are not declining

4 >0.2- more seedlings and saplings; vigorous resprouters; abundant and popular use species

Simpson's Permutation Index: values greater than 0.1 reveal a size frequency distribution that is steeper than expected for an exponentially declining population

Wiegand's Permutation Index : higher values indicate a discontinuous population

(After Wiegand *et al.* 2000)

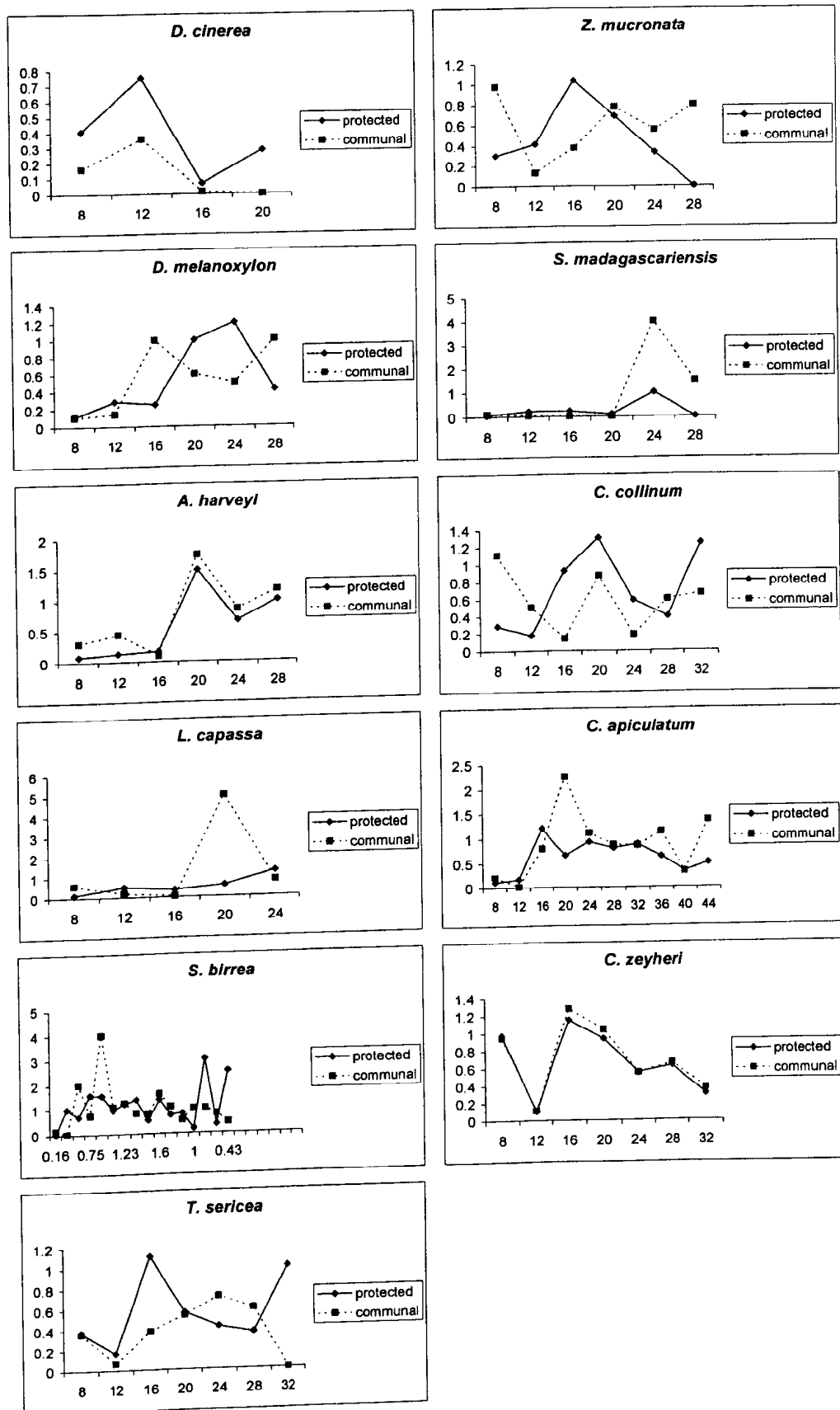


Figure 6. Quotients between woody plant frequencies in successive size classes. X-axis: diameter size class (cm); Y-axis: quotients.

similar trends in both protected areas and communal rangelands (Figure 6 on page 83). *S. birrea* was the most ‘unstable’.

3.4 DISCUSSION

This study presents evidence that certain savanna woody plant species appear to change their growth allocation strategy, at a generally consistent height, from a strategy focused on height gain to one showing a reduced height increment relative to diameter. This slowing in height gain may be linked to an alternative allocation of resources, i.e. with emphasis instead on reproduction, root extension or belowground biomass storage. The approximately 3 m height at which this switch in resource allocation was found to occur (ca. 10 cm in stem diameter) is in agreement with previous studies that have proposed that only once this height has been attained and savanna woody plants are less vulnerable to damage by fire, can resources be effectively allocated for reproduction (Trollope 1984, Higgins *et al.* 2000, Archibald & Bond 2003, Wilson & Witkowski 2003), with the costs of reproduction being particularly high in nutrient-poor ecosystems. Yet, for other species under study, there was no obvious size-related shift in proportional height to stem diameter growth increment. These tended to be the more multi-stemmed species, of a shorter stature. The two species showing the most uniform growth allocation across plant size range, *Combretum collinum* and *Combretum zeyheri*, were also the most multi-stemmed of the study species.

It is during the most vigorous growing sapling stage that differences in the growth strategies of woody plant species - to survive damage and reach reproductive maturity - are likely to be most evident (Kohyama & Hotta 1990). Yet, in a contrast of a common ‘small plant’ size range, the savanna woody plant species of this study were found to be broadly similar in their growth in height relative to stem diameter. Interestingly, the saplings of rain forest tree species have been found to show a similar lack of allometric variability despite differing in their tolerance to shade. Contrasts between the saplings of different Amazonian oligotrophic lowland rain forest species (Coomes & Grubb 1998) and of Indonesian old growth tropical rain forest species (Kohyama & Hotta 1990) found

that species did not differ substantially in the slopes of their height to stem diameter allometric relationships. This lack of plasticity was interpreted as suggestive of constraints on assimilate allocation. Coomes & Grubb (1998) warn, however, that the sapling height range used in these studies may be insufficient to test for significant differences among slope parameters. The allometric coefficients of the present study indicate that savanna woody plant saplings invest more growth into diameter relative to height increment than their forest tree counterparts. Also, there was some evidence that the saplings of more multi-stemmed savanna species have a lower height relative to aggregate stem diameter increment than single-stemmed species. Importantly, resource allocation by savanna woody plants to belowground biomass is likely to be considerable. Stored resources enable woody plants to survive and recover following damage and the loss of aboveground biomass. Although harder to measure, resource allocation to belowground storage is an important element to be considered when assessing and contrasting growth strategies.

Of considerable interest is the observation that a greater height increment in savanna woody plant species during the sapling phase appears to be associated with a higher wood density (Niklas *et al.* 2003). The specific density of wood is closely related to mechanical properties of strength, such as elastic moduli, which describe resistance to static and impact bending, compression and tension (Enquist *et al.* 1999). The allometric relationship between height and stem diameter may therefore be more closely related to the tensile strength of the wood and resistance to wind damage than to a saplings tolerance of shade or disturbances. Allocation to tissue density entails a trade-off in growth rate: species that allocate less biomass to their stems (light woods) increase in basal diameter faster than species that allocate more to stems (dense woods) (Enquist *et al.* 1999). As *Sclerocarya birrea* has a considerably lighter woody density than the other study species, it is possible that it grows the fastest, with growth during the sapling phase largely in stem diameter (and probably also in belowground biomass including extensive roots for stability and increased access to water). At some threshold stage, when the stem diameter can support it, growth is then shunted into rapid height gain to escape the flame (or browse) zone. The scarcity of sampled *S. birrea* individuals

of 2 to 4 m in height in both protected areas and communal rangelands could be evidence of such a growth strategy, with plants growing rapidly through this height range during favourable periods. The current study is, however, not able to support inferences made about the relative growth rates of these savanna woody plant species. With the exception of *S. birrea*, it is the species displaying two distinct growth phases that during their sapling phase have a larger height gain relative to diameter growth, in contrast to those species with an apparently uniform growth pattern. Yet, as plants are able to adapt their allocation strategies in response to resource availability, it is important to acknowledge that allometric parameters are not rigid descriptors of species and that the flexibility with which resources are allocated to growth versus storage remains poorly understood (Coomes & Grubb 1998).

At face value, the cumulative evidence of this study does not strongly support the hypothesis that episodic recruitment has largely shaped the population structures of these savanna woody plant species. However, it is plausible that episodic recruitment events have been masked by other factors such as growth suppression. Rohner & Ward (1999) found that browsing by herbivores delayed the growth of young trees of *Acacia* species by suppressing tree height to a level accessible to them. This resulted in a smoother size distribution than for unbrowsed populations that showed evidence of interrupted recruitment. Although the more obvious effect of browsing is height suppression, the loss of aboveground biomass will reduce subsequent growth in stem diameter. Repeated fires can have a similar effect, resulting in savanna woody plant seedlings persisting for many years as suppressed juveniles, with stems continuing to resprout following burning and the loss of aboveground biomass (Trollope 1984, Bond & van Wilgen 1996). Crucially, size structure may be a poor indication of episodic recruitment if diameter classes do not reflect age. The assumption of constant growth from one size class to the next across the entire size class range is simplistic and likely to confound interpretations, particularly in semi-arid and arid savanna ecosystems where woody plant demography is characterised by irregular growth in response to the incidence of favourable conditions (Wiegand *et al.* 2000). Therefore, several potentially interacting factors make the interpretation of population size

distributions fraught with complications. At a methodological level, the slope of a size class distribution depends not only on species traits and the disturbance history of sampled sites, but also on the choice of size class interval and the stem size range selected (Coomes *et al.* 2003).

Most of the study species had population structures defined by the various descriptive indices as deviating from a monotonically declining distribution curve, with a steeper than expected attenuation in woody plant numbers with increasing stem diameter size. This could be a consequence of a high mortality of small plants and/or the suppression of growth into successive stem diameter size classes as a consequence of limited water and nutrient availability or as a result of damage to aboveground biomass. Quotient plots confirmed that many of the species had populations that were relatively 'unstable', suggesting irregular growth and/or recruitment. *S. birrea*, of all the study species, had a population structure that could be interpreted as being reflective of episodic recruitment. However, irregular growth may translate into a comparable population structure and there was some evidence, particularly in protected areas, that browsing or fire may have inhibited growth into larger diameter size classes. *C. zeyheri*, *Ziziphus mucronata* and *Dichrostachys cinerea* were the species with the most 'even' size class distributions, indicating more regular recruitment, constant growth between size classes or a lower rate of mortality.

In general, woody plant allometry and population structure of the study species did not differ substantially with land use. This indicates that either different factors, e.g. browsing by livestock and fuelwood harvesting in communal rangelands or wild herbivores and fire in protected areas, have similar effects or that these have only a minor modifying effect on woody plant demography. In all likelihood, recruitment, growth and mortality of these semi-arid savanna woody plant species are driven primarily by regional rainfall patterns, over and above the impacts associated with particular land uses. It would be interesting to contrast the predominantly broad-leaf species selected for this study with fine-leaf (*Acacia*) savanna woody plant species of the same region.

Referring back to the study's aims, the findings suggest that the selected savanna woody plants can be divided into two broad groups: (i) those species that appear to change their growth allocation strategy during their life histories, with an emphasis on height gain during the period that they are most vulnerable to damage, and (ii) those species that appear to have a more uniform height relative to stem diameter growth increment across their entire size range, with a relatively greater diameter increment and perhaps more belowground biomass accumulation. During the sapling phase, only a small degree of variation was perceptible between species in the allometric relationship of height to stem diameter. Yet, there was some evidence to suggest that species-specific characteristics, such as wood density and the degree of branching, are associated with differences in woody plant allometry and apparent growth strategies. Finally, although several of the savanna woody plant species of this study were described as having relatively discontinuous and uneven population structures (in contrast to 'healthy' continuously recruiting natural forest populations), there was no conclusive evidence to suggest that their population structures were primarily shaped by irregular recruitment events. However, caution must be exercised when drawing conclusions from size distributions about the relative importance of factors in shaping population structure. Further investigation would be required to separate the influence of irregular growth, with size therefore not reflecting age, from the factors influencing recruitment and mortality.

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CHAPTER 4

Aspects of the Seedling Niche: Determinants of Woody Plant Establishment Success in an African Savanna



A recently emerged marula *Sclerocarya birrea* seedling, surrounded by grass and dried leaves, with pale green cotyledons and 2 pairs of leaves.

Abstract

Seedling establishment is widely considered to be one of the strongest filters determining subsequent savanna woody plant recruitment and demography. It is during this life history stage that plants are most vulnerable to environmental conditions and damage. Yet, little is known about the factors that either support or limit seedling establishment. Such an understanding has considerable implications for predicting and managing the balance between woody and herbaceous vegetation in response to intensive utilisation or climate change. A factorial experiment assessed the influence of grass competition (or facilitation) and herbivory on seedling emergence and survival over two growing seasons. Supporting field surveys recorded the microsite conditions associated with seedlings of different species and size. The experimental study provides strong evidence that, although not entirely preventing establishment, grass cover reduces both the number of emergent and surviving seedlings. Seedling predation during the winter period, presumably by rodents, had the highest impact on seedling survival. Seedling size was influenced by an interaction between grass treatment and herbivory. The field surveys revealed a recruitment pulse for all woody plant species following well above-average rainfall. Most seedlings, especially the smallest, were found beneath the canopies of other woody plants. Seedlings of this size were less numerous in communal rangelands compared with protected areas and in a site that had recently burnt. The majority of seedlings grew in microsites with relatively little grass cover. Evidence of seedling herbivory was more prevalent for seedlings growing in sub-canopy microsites than for seedlings growing in inter-canopy areas. The experimental results of this study together with the findings of the seedling field surveys, confirm herbaceous cover to be an important determinant of seedling establishment success, both directly through competition for water and indirectly by affecting seedling exposure to herbivores.

Keywords: grass competition; land use; rodent predation; seedlings; sub-canopy; woody plant recruitment

4.1 INTRODUCTION

“In plant ecology, the action is in the transition from seeds to seedlings. What comes later is history.” (Harper’s maxim (1977))

Any change in the distribution and abundance of woody plants within savannas is ultimately dependent on the recruitment of individuals into a population. “The spatial and temporal patterns of plant recruitment processes represent the integrated effect of biotic and abiotic environments on the patterns and processes of seed dispersal and germination and the emergence, growth and establishment of seedlings” (Grubb 1977). Therefore, any factors that alter seed availability, dispersal and seedling establishment are critical to woody plant population demographics (Grubb 1977, Harper 1977, Weltzin & McPherson 1999, Scholes & Archer 1997, Wiegand *et al.* 2000).

Under a variable climate the conditions conducive to the recruitment of certain savanna woody plant species occur very infrequently, requiring the coincidence of several favourable circumstances, including adequate rainfall and temporal gaps in browsing pressure or fire frequency (Moss 1996). Many species do not have a dormant seed bank that would allow them to successfully establish under these sporadically favourable conditions (Silvertown & Lovett Doust 1993). Instead, they may have populations of ageing seedlings, some of which might grow to reproductive maturity should conditions or disturbance events permit a sequence of temporary releases from the dominant factors that suppress them (Grime & Hillier 1992, Prins & van der Jeugd 1993, Silvertown & Lovett Doust 1993, Scholes & Archer 1997). This has been termed the “storage effect”, where overlapping generations of previously established seedlings result in strong recruitment when conditions are favourable (Chesson & Warner 1981).

Generally, savanna woody plant species are thought not to be seed-limited (Lamont *et al.* 1993), even though seed production may be highly variable and a considerable proportion of seeds parasitised or eaten (Gutteman 1994, Keesing 2000, Wiegand *et al.* 2000, Witkowski & Garner 2000, Wilson 2002). In heavily

utilised savanna woodlands, frequent damage to woody plants from browsing, fire or live wood harvesting may additionally limit seed production (O'Connor 1991, Erewijn & Verhoeven 1995, Milton 1995, Chapter 2). Instead, it seems that the success or failure of seedling establishment is widely considered to be of more importance in limiting woody plant recruitment, since plants are most vulnerable during this life-history stage to environmental conditions and damage (Harper 1977, Clark *et al.* 1998). Once seedlings are established they show a high degree of resilience, with fire, herbivory and dry periods inhibiting growth but rarely resulting in mortality.

Establishment success is an indicator of the suitability of a site, with the spatial distribution of seedlings integrating seed dispersal with the critical post-dispersal processes of seed survival, germination and early seedling growth and survival. Harper *et al.* (1961) introduced the term "safe sites" to describe small-scale environmental heterogeneities that create spatial variance in recruitment opportunities. Soil environments are highly heterogeneous and the heterogeneity of the microenvironment and subtlety of germination requirements determines the number of seedlings and their variety. Grubb's (1977) "regeneration niche" described temporal refuges in recruitment that promote coexistence between species when the conditions favouring the recruitment of one species differ from those of another, thereby reducing competition between the two. However, as Higgins *et al.* (2000) state: "Little is known about the regeneration niches of savanna woody plants" and there is little consensus in the literature as to the relative importance of various factors in facilitating or preventing seedling establishment. Probably this is because species differ in their requirements and tolerances, with the importance of factors additionally shifting in relation to the stage of seedling development. In very few cases have the factorial experiments been carried out to determine which variables and their interactions, limit establishment in a given circumstance (Clark *et al.* 1999).

There is little doubt, however, that soil moisture availability is the most important factor determining the abundance of young seedlings in semi-arid savannas (Skarpe 1990, Grundy *et al.* 1994, Erewijn & Verhoeven 1995, O' Connor 1995,

Hoffman 1996, Wilson & Witkowski 1998, Rohner & Ward 1999, Wiegand *et al.* 2000). Successful establishment, following germination, occurs when there is adequate soil moisture for long enough to ensure that seedlings extend roots sufficiently to survive the first growing season (Walker & Janssen 2002). Many other factors that are considered important for establishment success can be linked to water availability. For several species, a higher incidence of seedling establishment beneath the canopies of mature trees in contrast to the direct sunlight of inter-canopy areas may be a consequence of reduced solar irradiance and soil temperatures resulting in smaller fluctuations of soil moisture (Grundy *et al.* 1994, O'Connor 1995, Weltzin & McPherson 1997). Seedlings growing in sub-canopy environments may additionally be supported by higher microbial biomass and soil organic concentrations, greater mineralisable nitrogen and possibly protection from fire or herbivory (Hochberg *et al.* 1994, O'Connor 1995, Scholes & Archer 1997, Olf *et al.* 1999).

The frequently higher herbaceous production beneath tree canopies has similarly been linked to the lower soil temperatures and greater fertility (Smith & Goodman 1986, Belsky *et al.* 1989, Weltzin & Coughenour 1990, Belsky 1994). Young seedlings may compete with grass for limited water, nutrients and light and a high grass biomass has been shown in some cases to reduce seedling emergence, growth and survival (Walker *et al.* 1981, Knoop & Walker 1985, Gill & Marks 1991, Erewijn & Verhoeven 1995, O'Connor 1995, Wilson 2002). Yet, other studies have found seedling establishment to be unaffected by herbaceous biomass (Clarke & Davison 2001) or even facilitated through an associated reduced soil moisture evaporation and protection from herbivores (Brown & Archer 1989, Milton 1995, Scholes & Archer 1997, Olf *et al.* 1999). Grass may have an indirect effect, more pronounced in mesic savannas, of increasing the fuel load and subsequent fire frequency and intensity, resulting in the mortality of young seedlings (Trollope 1984, Hochberg *et al.* 1994). Under such circumstances, heavy grazing will reduce grass cover and enable the establishment of seedlings of some woody species and other previously established seedlings to escape fire suppression (Skarpe 1990, Smit 1996, Witkowski & Garner 2000, Rocques *et al.* 2001, Walker and Janssen 2002, van Langevelde 2003).

When seedlings are capable of establishing and growing under canopies with conditions of low irradiance (and frequently a high grass biomass), they may form a persistent seedling bank. However, seedling growth rates beneath mature plants have been found to be slower than for those of seedlings in direct sunlight (Grundy *et al.* 1994), with seedlings more etiolated (O'Connor 1995) and probably taking longer to reach reproductive maturity should they survive. Smith & Goodman (1986) found that woody plants in semi-arid savannas fail to recruit under the canopies of mature trees resulting in a pattern of regularly dispersed trees. Some species are thought to be entirely intolerant of the low irradiance conditions beneath canopies (Smith & Shackleton 1988, Smit 1996), for instance Yeaton (1988) reported that seedlings of members of the Combretaceae established only in open areas in semi-arid savannas. High seed predation may also limit seedling establishment near parent plants despite greater seed availability and germination (Silvertown & Lovett Doust 1993, Moss 1996, Radford 2002). Herbivory, by ungulates, rodents and insects, has been found to suppress seedling growth (Moss 1996, Shaw 2002, Augustine & McNaughton 2004), but unless seedlings are very young (less than a year old and not yet established), is considered unlikely to induce mortality (but see Gill & Marks 1991, Keesing 2000).

While recognising that many factors are likely to be involved, and to interact, in influencing seedling establishment success, the focus of this study was on the effect of grass cover and herbivory on seedling establishment. A field factorial experiment tested the hypotheses that seedling emergence and survival is:

1. Lower in plots containing live grass than in plots with either (i) no grass cover and therefore no competition for soil moisture, or with (ii) dead grass, i.e. removing the competitive influence of grass cover while retaining the shading effect.
2. Higher in plots protected from herbivory (by ungulates and rodents).

Supporting field observations investigated seedling distribution and microsite characteristics to determine whether the conditions conducive to seedling survival

and establishment varied for seedlings of different species or size. The hypotheses tested were:

3. Seedlings are more numerous beneath the canopies of 'parent' plants than in inter-canopy areas.
4. Seedlings are less numerous in an area recently burnt or heavily grazed in comparison to areas with less recent disturbance.

Being able to define distinguishing features of supportive seedling environments would impart a level of understanding as to where in a landscape seedling establishment is most likely to be successful. This understanding is important for the management and rehabilitation of intensively utilised savanna woodlands.

4.2 METHODS

4.2.1 Study area and approach

The study region was located within the Bushbuckridge area (centering on 31° 17' E; 24° 39' S) of the South African 'lowveld' of the Limpopo Province. The area was delimited by Acornhoek settlement in the west and Manyeleti Reserve bordering the Kruger National Park in the east (Figure 1 on page 100).

The region is characterised by low rainfall (ca. 650 mm per annum in the west; ca. 550 mm per annum in the east), concentrated in the summer season (October to May), largely in the form of convectional thundershowers. Intra-annual rainfall variation is greater than 35% (Schulze 1997) and intra-seasonal drought is common with more prolonged drought occurring as often as every 3.5 years. Mean annual temperature is 22° C and mean daily maxima are approximately 30° C in January and 23° C in July.

The topography of the study region is gently undulating. Soils are underlain by granitic gneiss with local intrusions of gabbro. Vegetation of the region is broadly classified as Mixed Lowveld Bushveld and is dominated by species of the Combretaceae (Van Rooyen & Bredenkamp 1996).

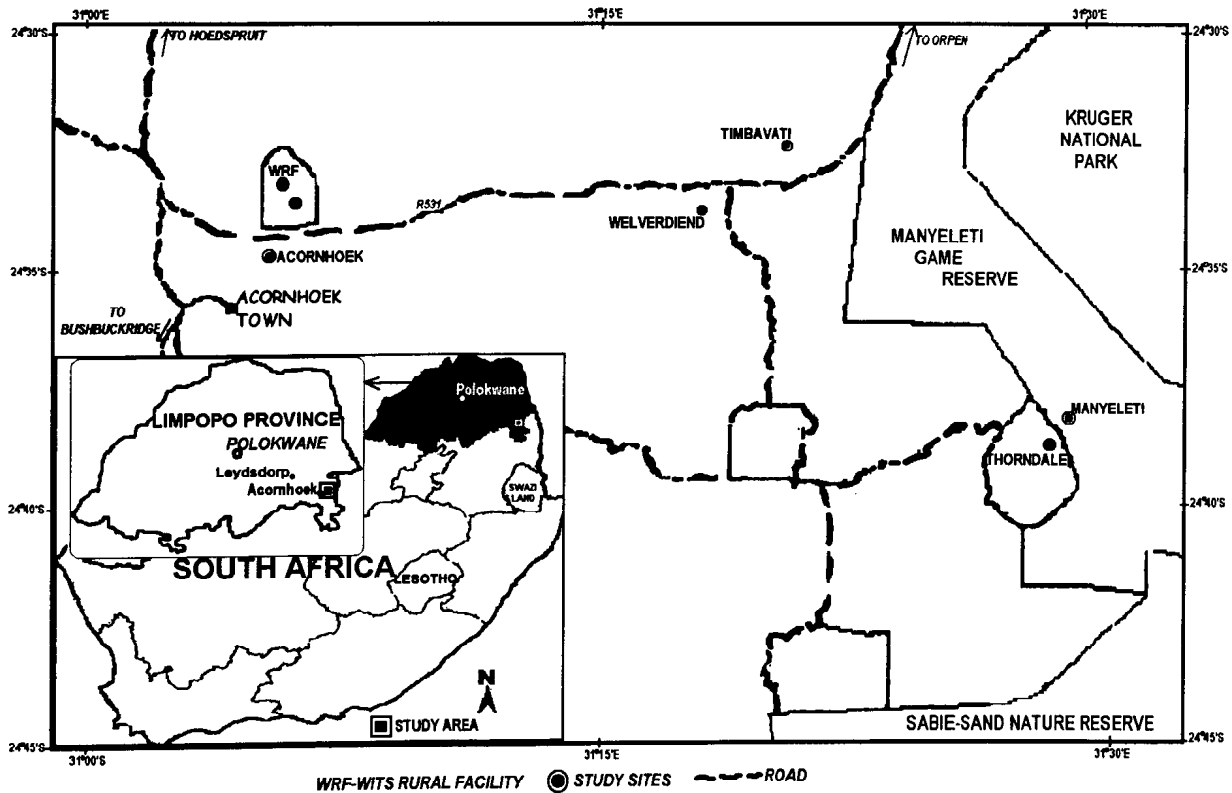


Figure 1. Map of the Bushbuckridge study region, Limpopo Province, South Africa. Paired study sites in communal rangelands and protected areas are indicated. The additional site in the Wits Rural Facility sampled an area recently burnt.

Additionally, the marula *Sclerocarya birrea* and sickle bush *Dichrostachys cinerea* contribute considerably to woody biomass within the region (Shackleton 1997). There have been several decades of intensive utilisation of communal grazing lands resulting in an alteration of woodland structure described as “short sparse woodland” by Edwards’ (1983) physiognomic classification. Adjacent protected areas have considerably denser woody vegetation and are classified as “short bushland”.

A field factorial experiment was established in October 2001 at Wits Rural Facility, in a lightly wooded and relatively flat area. The experimental study was conducted over two wet seasons from seed planting in December 2001 to a final measurement of seedlings in March 2003. Small indigenous ungulates on the

property included impala, duiker and bushbuck. Rodent species might include *Rabdomys pumilio*, *Aethomys chrysophilus* and *Saccostomus campestris* (Mushasha 1999). Mean rainfall (recorded close to the experimental site) was during the 2001/2 wet season (July – June) close to the average (583 mm) and in the 2002/3 wet season well below average (288 mm).

Seedling surveys were undertaken in communal rangelands surrounding the settlements of Acornhoek, Thorndale and Welverdiend. Each was paired with a site located less than 2 km away, in the woodlands of adjacent protected areas - Wits Rural Facility, Manyeleti and Timbavati, respectively. The contrast between communal rangeland and protected area sites enabled an assessment of whether occurrence and patterns of seedling establishment were influenced by factors specific to either land use, e.g. grazing livestock and wood harvesting in communal rangelands and browsing indigenous ungulates in protected areas. An additional area within Wits Rural Facility, burnt shortly before the onset of the 2002/3 wet season, was surveyed to assess the impact of fire on seedling survival. Seedling surveys were carried out towards the end of the 2002/3 wet season, two to three months after probable seed germination. They therefore followed the period of high mortality in the post-germination phase and are likely to have monitored initial establishment of the current season's seedling cohort. Although rainfall received during the 2002/3 wet season was well below average, there had been no 'dry' periods, i.e. exceeding 30 days without rainfall (Hoffman 1996, Higgins *et al.* 2000), prior to the survey.

4.2.1.1 Field factorial experiment

The experiment was designed to determine the influence of grass cover and herbivory on woody seedling emergence and establishment. The factorial set up was as a single, randomised block, but with each treatment represented within both the 'rodent-accessible' and 'open' area (Figure 2 on page 102). Plot size was 1.5 x 1.5 m, with the overall enclosure constituting 20 contiguous (4 x 5) plots and covering an area of 45 m². Each grass treatment had three replicates within the 'protected' area from which both ungulates and rodents were excluded and a

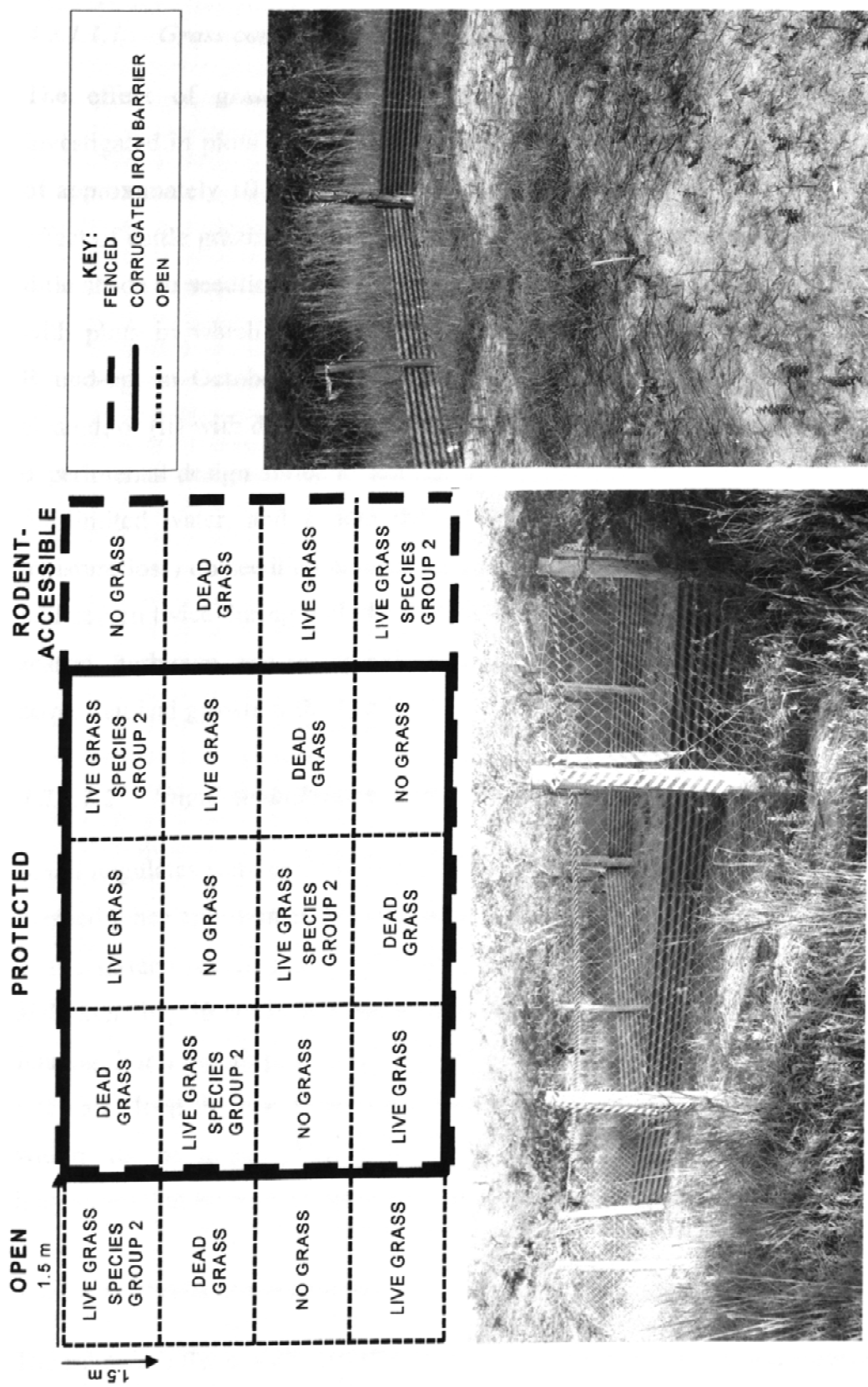


Figure 2. The factorial experiment designed to assess the influence of herbaceous cover on woody plant seedling emergence and survival, together with the (interactive) effect of herbivory (by small browsing ungulates and rodents).

single replicate within both the open and rodent-accessible areas. Treatments were applied to the entire plot area.

4.2.1.1.1 *Grass competition or facilitation*

The effect of grass cover on seedling emergence and establishment was investigated in plots containing established grass tufts. Grass was cut to a height of approximately 10 cm during the early wet season (November) to simulate the effect of cattle grazing in communal rangelands. Grass cut to this height provides little shade to seedlings (O'Connor 1995). These live grass plots were contrasted with plots in which all herbaceous cover had been killed (using a herbicide, Round-up, in October prior to the growing season) and either (i) completely cleared, or (ii) with dead grass left *in situ* (initially upright, later decumbent). The experimental design aimed to test respectively, the influence of grass competition for limited water, and a potential facilitative influence (shading and reduced moisture loss) on seedling emergence and survival. Follow-up grass clipping was undertaken twice during both the first and second wet seasons. Prior to the second season, herbicide was re-applied in the relevant plots, to kill herbaceous grass cover that had grown in the interim.

4.2.1.1.2 *Ungulate and rodent herbivory*

Small ungulates were excluded from all but the four 'open' plots by a robust wire-meshed fence approximately 1.2 m in height. Rodents were excluded from twelve of the sixteen fenced plots with corrugated iron sheeting, embedded in concrete and extending 30 cm below and 50 cm above the ground surface, external to the fencing. For a month prior to seed planting, rodent poison was placed in dishes at intervals along the corrugated iron 'barrier' to ensure that there were no rodents within its perimeter. Throughout the experimental period there were no indications that herbivores had gained access to the plots protected from them.

4.2.1.1.3 *Seeds and seedlings*

The relative influence of each treatment on seedling emergence and survival was tested for three species: *Sclerocarya birrea*, *Strychnos madagascariensis* and

Terminalia sericea. The emergence and survival of a further three species, *Combretum collinum*, *Dichrostachys cinerea* and *Ziziphus mucronata*, were assessed for plots with the live grass cover treatment only ('species group 2' in Figure 2 on page 102). The six study species were amongst the most abundant at Wits Rural Facility (Shackleton 1997) and represent a range of fruit sizes that differ in dispersal agents: *S. birrea*, *S. madagascariensis*, *Z. mucronata* are all fleshy-fruited and seeds are dispersed by mammals (including humans) and birds; *D. cinerea* has nutritious seed pods that are also dispersed by vertebrates; the two Combretaceae species, *T. sericea* and *C. collinum*, have winged fruits that are wind dispersed.

Seeds were planted during the early wet season (12th–14th December 2001). The high amount of rainfall received during the previous month (270 mm, 2½ times the monthly average) made the ground ideal for seed sowing. The seeds were collected from more than ten individuals of each woody species within the region. All seeds were examined and only those appearing intact were used. *C. collinum* and *D. cinerea* seeds were removed from fruits and the wing surrounding *T. sericea* fruits was removed and opposite ends of the fruit cut to expose the seed. To ensure ready germinability, the seeds of all species were soaked in warm water for 3 hours and subsequently planted at a soil depth of ca. 2 cm. Within each plot, 48 seeds of each of the three species were arranged in a 12 x 12 grid with an inter-seed spacing of 10 cm. There was 40 cm between the outer seeds of one treatment plot and those of the adjacent one. Where a seed's grid position coincided with a grass tuft, the seed was planted in the soil immediately next to the tuft. Care was taken during seed planting to minimise disturbance of the original soil structure.

Supplemental watering (15 l. per plot), carried out after each three day period during which no rain had fallen, reduced the likelihood of desiccation during the vulnerable post-germination stage, i.e. from time of seed planting (December, 2001) until the end of the first wet season (March, 2002). Each addition was equivalent to a rainfall event of ca. 3.75 mm. The cumulative supplementation of water was 150 mm, resulting in an effective total of 691 mm, including rainfall (92% of the seasonal mean), over the growing period (October to April). Plots

were watered shortly before sunset to reduce evapo-transpiration and any detrimental effects of watering in combination with high irradiation.

Emerging seedlings were counted at weekly intervals during the first growing season. Each emerging seedling was individually marked and monitored to distinguish the timing of emergence and location within the plot, enabling the fate and growth of individual seedlings to be tracked. The size of surviving seedlings, i.e. height, basal stem diameter and the number of leaflets, was recorded at the end of the first growing season (March 2002) and at the beginning (November 2002) and end of the following one (March 2003).

4.2.1.2 *Seedling field surveys*

Field surveys of woody plant seedlings were carried out in February and March 2003 (late summer). In each of the study sites, searches were made for seedlings within a woodland area that was similar in appearance of the remainder of the site. For communal rangeland sites, surveys were made in woodland that had not been cleared for agricultural fields and appeared to be relatively undisturbed. Seedlings were easy to detect amongst grass that was desiccated following the hot summer season. Long grass was searched particularly carefully for concealed seedlings. The size of the area searched differed for each site, being determined by the area covered as thoroughly as possible by two field workers during a period of four hours.

The species and size of each seedling encountered was recorded, as well as information on the microsite environment, including:

- whether the seedling grew beneath the canopy of a tree or in inter-canopy areas (and if beneath a canopy, the canopy tree species);
- the distance to the nearest potential mature 'parent' plant (when one could be located);
- grass height, aerial grass cover (using Walker's (1976) scale) and the dominant grass species, within a 1 m² quadrat centred on the seedling;

- the relative amount of litter cover present, defined as ‘absent’, ‘little’ or ‘lots’;
- soil relative ‘moistness’, defined as ‘moist’ or ‘dry’.

The soil around seedlings was carefully excavated to distinguish between seedlings originating from root and suckers growing from the root crowns of other plants. Measurements of seedling size were: height (measured from the ground surface to seedling apex), stem diameter and the number of leaflets. Seedling stem diameter was measured just above the soil surface with callipers. Only a few seedlings had more than one stem. For these the number of stems was recorded, the diameters of all stems were measured and a composite stem diameter determined by calculating the cross-sectional areas of each stem, summing them and using this aggregate stem area to calculate the effective seedling stem diameter. By definition seedlings were less than 0.5 m in height and smaller than 1 cm in stem diameter. Seedling age was estimated as being either from the current wet season (< 1 year old), the previous season (1 to 2 years old) or older and belonging to a multi-age group (> 2 years). Indicators of seedling age were the presence of cotyledons, the degree of stem woodiness and seedling size. Seedlings from the current season were unmistakable from the presence of cotyledons and/or stems that were green and flexible. Seedlings defined as being 1 to 2 years in age were distinguished from those considered older by being less woody and having a smaller stem diameter (< 0.3 cm). The seedlings of all species were considered to have been reliably aged in this way. Any damage to seedlings was recorded, i.e. the presence of fire scars, evidence of herbivory (ungulate or insect) or trampling (revealed by caten or broken stems and leaves).

Previously collected data on the densities and population structure of woody plant species in each of the sites in which the seedling surveys were conducted enabled a contrast between the relative abundance of seedlings and reproductively mature individuals of woody plant species. At each site, the dimensions of all established woody plants within eight, 4 by 100 m, transects were measured (refer to Chapter 2 for further details on data collection). Following Shackleton (1997), ‘mature’

plants were defined as being those taller than two thirds of the maximum height of that species (calculated as the mean of the ten tallest plants).

4.2.2 Statistical Analyses

4.2.2.1 Field factorial experiment

4.2.2.1.1 Seedling emergence and survival

Differences in the number of *S. birrea* and *T. sericea* seedlings, emerging and surviving, under each of the grass treatments was assessed with two-sample t-tests with assumed equal variances. Given the low power of the statistical tests (d.f. = 8), $\alpha \leq 0.1$ was considered statistically significant. More detailed analyses of the influence of experimental treatments on seedling emergence, survival and size, were possible for *S. madagascariensis*, the only species with a large number of emergent and surviving seedlings. The proportion of *S. madagascariensis* seedlings per plot that emerged and the proportion of emergent seedlings that were alive at the end of the experimental period were subjected to log-linear analyses to assess the influence of grass treatment as well as protection from small ungulates or rodents. Seedling survival at the end of the first and second growing seasons and following the intermediate dry winter period (April-October), were similarly assessed. All seedlings emerging were assumed to have done so from seed added for the experiment (individual seed/seedling location had been recorded) with no additional natural recruitment. Analyses were based on the reasonable assumption that seed germination and seedling survival was not influenced by position within a plot.

The log-linear analyses for both seedling emergence and survival (as the number of seeds planted or of the number of emergent seedlings, respectively) were carried out with generalised linear models using the appropriate procedures in R (v 1.7.1) freeware (similar to S-Plus) for a binomial error distribution and logit link function (Crawley 2002). Maximum likelihood (ML) estimation of model parameters was used. The analysis tested the dependence of seed or seedling fate on (i) grass treatment (at three levels: live grass, dead grass and cleared grass),

(ii) protection from ungulates and rodents (at three levels: protected, open to ungulates and rodents and accessible to rodents but not to ungulates), and (iii) the interaction between grass treatment and protection from herbivory. A model simplification process was followed to determine the ‘best fit’ model for the data, i.e. the model containing only those variables that resulted in a significant increase in deviance when removed (Crawley 2002).

4.2.2.1.2 *Seedling size*

The effect of grass treatment and protection from herbivores on *S. madagascariensis* seedling size at the end of the first and second growing seasons and following the winter period was tested using generalised linear modelling for a Gamma error distribution and inverse link function. The variables used to define seedling size were height, basal stem diameter and leaflet number. Mean seedling size per plot was used to avoid pseudo-replication. The influence of treatment on leaflet number was analysed using a poisson error function and a log link. Treatment effect on the number of leaflets per unit height, as an index of etiolation (O'Connor 1995), was additionally assessed. In all cases the response variable was found to be overdispersed, i.e. the probability distribution having a dispersion parameter different from one and a variance greater or less than expected from the mean (Quinn & Keough 2002). A more flexible quasi-likelihood (quasi-Poisson) model was therefore used to estimate the dispersion parameter from the data rather than restricting it to the value implied by the binomial distribution. An F test instead of chi-square test was used to determine whether the change in deviance resulting from the exclusion of a variable was significant. A single-factor ANOVA examined whether there was a size difference between seedlings that lived through the winter period and those that died.

4.2.2.2 *Seedling field surveys*

The number of seedlings of each woody plant species was compared between adjacent communal rangeland and protected area sites using a two-sample t-test with assumed equal variances. A Spearman Rank correlation tested whether the ratio of seedlings to mature plants across all species, differed with land use.

χ^2 tests (with Yates correction) assessed whether the ratio of seedlings to mature woody plants differed between communal rangelands and protected areas for each species. Subsequent analyses focused on the five species with a good representation of seedlings (> 50 seedlings). Generalised linear model analyses (following the methods previously described for a response variable with binomial error distribution and using a logit link function) assessed the probability of a seedling of a particular species or size (stem diameter size class) growing beneath the canopy of another woody plant as opposed to in inter-canopy areas. The number of seedlings occurring in sub-canopy and inter-canopy areas was compared with a two-sample t-test. The association of each of the recorded categorical environmental variables (grass cover, grass species, soil 'moistness' and leaf litter) with sub-canopy and inter-canopy seedling microsites was examined with generalised linear model analyses. A single factor ANOVA assessed whether grass height differed for sub-canopy and inter-canopy seedling microsites.

Stem diameter frequency distributions, with size class intervals of 0.2 cm, were constructed and Kolmogorov-Smirnov tests assessed whether seedling size distributions differed between land uses or for sub-canopy and inter-canopy seedling microsites. Single-factor ANOVA determined whether seedling size (height, stem diameter and the degree of etiolation) differed with land use or seedling microsite. A Kruskal-Wallis median test was used to compare leaflet number. The number of seedlings per species, size frequency distributions and other seedling size indices of the burnt site were similarly contrasted with those of the nearby non-burnt site.

4.3 RESULTS

4.3.1 Field factorial experiment

4.3.1.1 Seedling emergence and survival

Germination and seedling emergence occurred within 2 to 4 weeks following planting with *Strychnos madagascariensis* seeds taking the longest. For the three

species for which 720 seeds were planted, i.e. 240 seeds of each species for each of the three grass treatments, there was a 21.9% emergence of seedlings, with generally lower densities emerging and surviving in the plots with live grass than in those containing dead grass or no grass (Table 1 below).

Table 1. The proportion (%) of seedlings emerging and surviving after each season under each grass treatment, for the three principal study species: a) *Strychnos madagascariensis*, b) *Sclerocarya birrea* and c) *Terminalia sericea*. An equal number of seeds (n = 240) had been planted for each grass treatment. The number of seedlings emerging and surviving is shown in parentheses.

a. <i>Strychnos madagascariensis</i> (n_{total} = 416)	live grass	dead grass	no grass
Seedling emergence (Dec. 2001 - Jan. 2002)	49.2 (118)	61.3 (147)	62.9 (151)
Seedling survival (end of 1 st growing season - Mar. 2002)	94.1 (111)	95.2 (140)	98.7 (149)
Seedling survival (end of winter period - Nov. 2003)	62.2 (69)	77.9 (109)	67.1 (100)
Seedling survival (end of 2 nd growing season - Mar. 2003)	76.8 (53)	83.5 (91)	92.0 (92)
Seedling survival (over experimental period)	44.9	61.9	60.9
b. <i>Sclerocarya birrea</i> (n_{total} = 45)	live grass	dead grass	no grass
Seedling emergence (Dec. 2001 - Jan. 2002)	3.3 (8)	6.6 (16)	8.9 (21)
Seedling survival (end of 1 st growing season - Mar. 2002)	75.0 (6)	93.8 (15)	51.4 (11)
Seedling survival (end of winter period - Nov. 2003)	50.0 (3)	66.7 (10)	81.8 (9)
Seedling survival (end of 2 nd growing season - Mar. 2003)	66.7 (2)	80 (8)	77.8 (7)
Seedling survival (over experimental period)	25.0	50.0	33.3
c. <i>Terminalia sericea</i> (n_{total} = 12)	live grass	dead grass	no grass
Seedling emergence (Dec. 2001 - Jan. 2002)	0.9 (2)	1.9 (5)	1.9 (5)
Seedling survival (end of 1 st growing season - Mar. 2002)	100.0 (2)	40.0 (2)	100.0 (5)
Seedling survival (end of winter period - Nov. 2003)	0 (0)	50.0 (1)	100.0 (5)
Seedling survival (end of 2 nd growing season - Mar. 2003)	0 (0)	0 (0)	100.0 (5)
Seedling survival (over experimental period)	0.0	0.0	100.0

S. madagascariensis seedlings were the most abundant with 57.8% of planted seeds producing emergent seedlings in contrast to 6.3 % of *Sclerocarya birrea* seeds and 1.7% of *Terminalia sericea* seeds. Of the emergent seedlings, more than half (56.7%) of the *S. madagascariensis* seedlings survived the winter, while fewer *S. birrea* and *T. sericea* seedlings survived (37.8% and 41.7%, respectively). Significantly more *S. birrea* and *T. sericea* seedlings survived the

experimental period in plots cleared of grass than in those with live grass (t-statistic = -1.66, $P = 0.07$; t-statistic = -1.83, $P = 0.05$, respectively). The *T. sericea* seedlings surviving at the end of the experimental period were all in plots that had been cleared of grass. Significantly more *S. birrea* seedlings also survived in plots containing dead grass than in those with live grass (t-statistic = -1.98, $P = 0.04$). For the second group of species for which 240 seeds were planted within plots containing live grass: 3.9% of *Ziziphus mucronata*, 3.5% of *Dichrostachys cinerea* and 3.0% of *Combretum collinum* seedlings emerged. The low emergence ($n = 24$ for all three species) and negligible seedling survival (10 seedlings survived the first growing season, while none survived through the winter period) precluded these species from subsequent analyses.

Grass treatment influenced *S. madagascariensis* seedling emergence (Table 2 on page 112), with plots containing live grass having a significantly lower emergence rate than those cleared of grass ($P = 0.04$; rate of emergence: $49.2 \pm 16.6\%$ (SE) and $62.9 \pm 23.9\%$, respectively) (Figure 3 on page 113). There was no significant difference in emergence between plots containing dead grass and those from which all grass had been removed. Seedling emergence was not influenced by the level of protection from herbivory or by the interaction between grass treatment and herbivory.

The number of *S. madagascariensis* seedlings surviving after two growing seasons did not appear to be influenced by either grass treatment or protection. Similarly, there was no apparent treatment effect on the proportion of seedlings surviving at the end of the first growing season. During the winter period, exclusion of herbivores appears to have been influential for seedling survival. Plots accessible to rodents (but protected from ungulates) had considerably fewer surviving seedlings ($46.5 \pm 40.4\%$ (SE)) than plots protected from both rodents and ungulates ($75.3 \pm 29.9\%$) or plots open to both ungulates and rodents ($73.0 \pm 48.9\%$) ($P = 0.012$). Seedling survival during the second growing season was influenced by grass treatment and not by the level of protection from herbivory. A higher proportion of seedlings growing in plots with no grass survived ($92.0 \pm 48.9\%$) than those in live grass ($76.8 \pm 29.9\%$) ($P = 0.026$). Once

more, the proportion of seedlings surviving in plots containing dead grass ($83.5 \pm 40.4\%$) did not differ significantly from that of the cleared grass plots.

Table 2. Generalised linear model analysis of *Strychnos madagascariensis* seedling emergence and survival in response to grass treatment and protection from herbivory. The influence of treatments on seedling survival was assessed for (i) the proportion of emergent seedlings that were alive after two growing seasons and the proportion of seedlings surviving through (ii) the first growing season; (iii) the winter period; and (iv) the second growing season (G^2 is the change in deviance and Δ d.f. is the change in degrees of freedom resulting from removal of a parameter; a binomial error distribution and logit link function were used; bold $P < 0.1$).

	Model Term	F	P	G^2	Δ d.f.
Emergence	Grass(G) : Protect(P) (interaction)	1.95 (6)	0.49	3.41	8
	Protect (P)	2.04 (12)	0.17	7.80	2
	Grass (G)	3.34 (12)	0.07	11.03	2
	live (L) : 0.49 ± 0.17				
	dead (D) : 0.61 ± 0.24				
	cleared (C) : 0.63 ± 0.24				
	(L vs D: $P = 0.06$; L vs C: $P = 0.04$)				
Survival - Overall	Grass(G) : Protect(P) (interaction)	1.06 (6)	0.49	28.94	8
	Protect (P)	2.53 (12)	0.12	14.41	2
	Grass (G)	1.44 (12)	0.27	9.35	2
Survival - 1 st season	Grass(G) : Protect(P) (interaction)	1.75 (6)	0.26	12.28	8
	Protect (P)	1.17 (12)	0.35	2.92	2
	Grass (G)	1.38 (12)	0.29	3.15	2
Survival - Winter	Grass(G) : Protect(P) (interaction)	1.33 (6)	0.38	30.9	8
	Protect (P)	4.53 (12)	0.03	20.68	2
	protected (P) : 0.75 ± 0.23				
	rodent access (R) : 0.46 ± 0.43				
	open (O) : 0.73 ± 0.43				
	(P vs R: $P = 0.01$; R vs O: $P = 0.02$)				
	Grass (G)	1.19 (12)	0.34	7.86	2
Survival - 2 nd season	Grass(G) : Protect(P) (interaction)	1.08 (6)	0.48	12.87	8
	Protect (P)	0.47 (12)	0.63	1.58	2
	Grass (G)	3.58 (12)	0.06	7.89	2
	live (L) : 0.77 ± 0.30				
	dead (D) : 0.83 ± 0.40				
	cleared (C) : 0.92 ± 0.49				
	(L vs C: $P = 0.03$)				

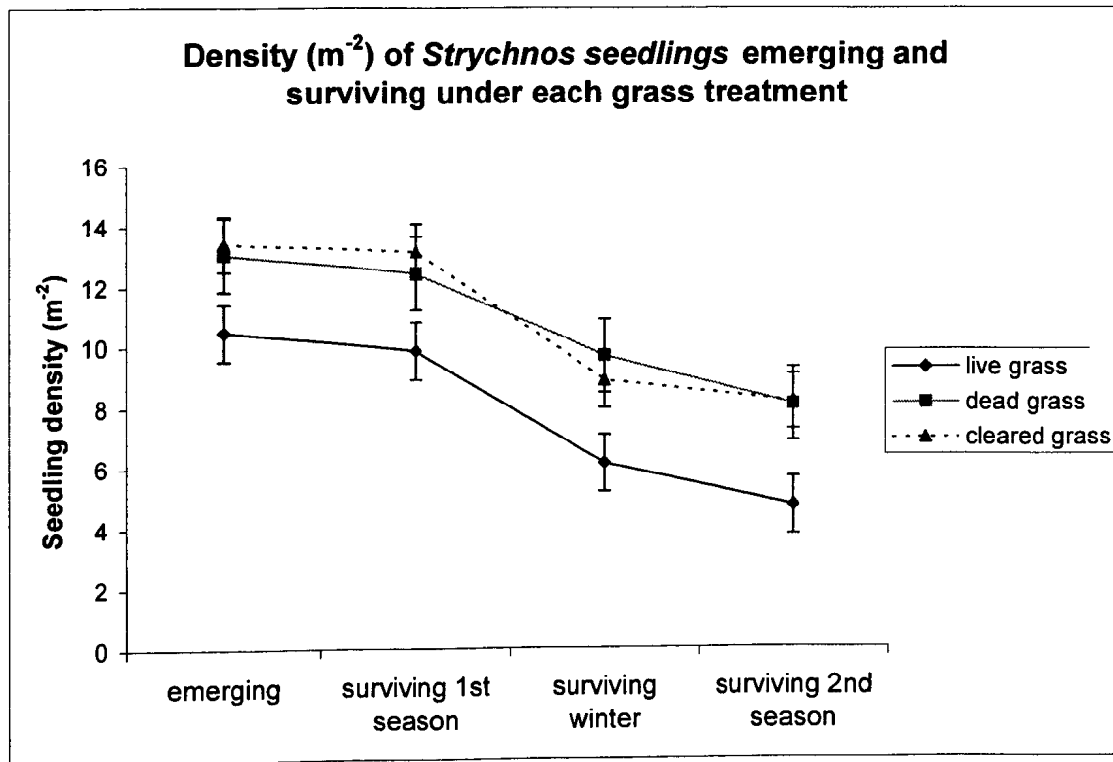


Figure 3. The number of *Strychnos madagascariensis* seedlings emerging and surviving in plots containing live grass, dead grass or cleared of grass. Standard error bars are shown.

4.3.1.2 Seedling size

An interaction between grass treatment and protection from herbivory influenced *S. madagascariensis* seedling size, with the effect of protection from herbivory contingent on grass treatment (Table 3 on page 114). Seedlings were shorter in plots exposed to herbivores (6.54 ± 0.02 cm) than in those with protection (10.75 ± 0.01 cm) ($P = 0.01$). Throughout the experimental period, seedlings exposed to herbivores had fewer leaflets than those growing in plots protected from rodents and both rodents and ungulates, this difference being most pronounced after the winter period and subsequent growing season. During the winter period, there were fewer leaflets per seedling in both open plots (59.8% fewer leaflets) ($P = 0.04$) and in those accessible to rodents (63.1%) ($P = 0.03$) in contrast to the leaflet number of seedlings in plots protected from herbivores. During the second growing season (as for the first growing season), the difference in leaflet number per seedling was most pronounced between seedlings exposed

Table 3. Generalised linear model analysis of the influence of grass treatment and protection from herbivory on *Strychnos madagascariensis* seedling size. The influence of treatments on seedling size (stem diameter, height and the number of leaflets per unit height) was assessed after two growing seasons. The influence of treatments on leaflet number is shown for both growing seasons and for the intermediate winter period (G^2 is the change in deviance and Δ d.f. is the change in degrees of freedom resulting from removal of a parameter; a binomial error distribution and logit link function were used; bold $P < 0.05$).

	Model Term	F	P	G^2	Δ d.f.
Stem diameter	Grass(G) x Protect(P)	5.89 (6)	0.02	0.3	8
	Protect (P)	2.32 (12)	0.14	0.10	2
	Grass (G)	0.14 (12)	0.87	0.01	2
Height	Grass(G) x Protect(P)	7.9 (6)	0.01	1.02	8
	Protect (P)	5.92 (12)	0.02	0.56	2
	Grass (G)	0.42 (12)	0.67	0.07	2
	protected (P): 10.75 ± 0.01				
	rodent access (R): 8.31 ± 0.02				
	open (O): 6.54 ± 0.02				
	(P vs O: $P = 0.01$)				
Leaflet number - 1st season	Grass(G) x Protect(P)	6.82 (6)	0.02	15.49	8
	Protect (P)	13.01 (12)	0.001	11.72	2
	Grass (G)	0.02 (12)	0.98	0.46	2
	protected (P): 19.89 ± 0.05				
	rodent access (R): 15.67 ± 0.11				
	open (O): 16.80 ± 0.13				
	(P vs R: $P = 0.05$; P vs O: $P < 0.001$)				
Leaflet number - winter	Grass(G) x Protect(P)	4.39 (6)	0.04	36.65	8
	Protect (P)	5.18 (12)	0.02	19.93	2
	Grass (G)	1.32 (12)	0.3	7.52	2
	protected (P): 30.11 ± 0.08				
	rodent access (R): 18.0 ± 0.21				
	open (O): 19.0 ± 0.20				
	(P vs R: $P = 0.03$; P vs O: $P = 0.04$)				
Leaflet number - 2nd season	Grass(G) x Protect(P)	4.45 (6)	0.04	25.56	8
	Protect (P)	4.96 (12)	0.03	14.13	2
	Grass (G)	0.09 (12)	0.91	0.46	2
	protected (P): 26.67 ± 0.08				
	rodent access (R): 20.0 ± 0.17				
	open (O): 15.67 ± 0.19				
	(P vs O: $P = 0.02$)				
Etiation (leaflets per unit height)	Grass(G) : Protect(P)	2.18 (6)	0.18	0.92	8
	Protect (P)	0.39 (12)	0.69	0.07	2
	Grass (G)	3.58 (12)	0.06	7.89	2
	live (L): 2.18 ± 0.04				
	dead (D): 3.60 ± 0.05				
	cleared (C): 3.45 ± 0.05				
	(L vs D: $P = 0.004$; L vs C: $P = 0.006$)				

to herbivory by both ungulates and rodents (59% fewer leaflets) in contrast with those protected from herbivory ($P = 0.02$). Seedlings growing in association with live grass were taller, with a smaller stem diameter and fewer leaflets per unit

height (i.e. relatively etiolated) than those seedlings growing in plots in which grass had been killed or cleared. This effect was most evident during the first growing season (ANOVA: $F_{2,376} = 12.08$, $P < 0.0001$; $F_{2,376} = 3.09$, $P = 0.047$; $F_{2,376} = 9.94$, $P < 0.0001$, for height, stem diameter and leaflet number, respectively).

There was a clear difference in the size of seedlings surviving the winter period and those that did not, with all measures of size at the end of the first growing season larger for seedlings that survived than for those that did not (Table 4 below). The degree of etiolation did not differ for seedlings that survived and those that did not.

Table 4. Comparison of size of *Strychnos madagascariensis* seedlings (mean $\pm$ SE) at the end of the first growing season of seedlings that survived through the dry winter period and those that did not (ANOVA, bold P values indicate significant difference).

	Survived (n=258)	Died (n=121)	$F_{1,377}$	P
Height (cm)	8.96 $\pm$ 0.24	6.89 $\pm$ 0.37	22.45	< 0.0001
Stem diameter (cm)	0.15 $\pm$ 0.01	0.12 $\pm$ 0.01	20.81	< 0.0001
Number of leaflets	18.24 $\pm$ 0.53	11.85 $\pm$ 0.70	14.25	0.0002
No. leaflets/height	2.25 $\pm$ 0.10	2.72 $\pm$ 0.19	1.68	0.196

4.3.2 Seedling field surveys

4.3.2.1 Land use contrast

A total of 809 seedlings were located during the field surveys. The species represented by the most abundant seedlings were *S. birrea*, *T. sericea*, *Diospyros mespiliformis*, *Dalbergia melanoxylon* and *S. madagascariensis*. Most of the youngest seedlings, i.e. those with cotyledons, from the current (2003) season were *S. birrea*. Nearly all (97.8%) seedlings were single-stemmed. For all woody plant species, seedling numbers did not differ significantly with land use when paired protected and communal rangeland sites were contrasted.

The relative abundance of seedlings and plants considered to be reproductively mature differed between communal rangelands and protected areas for several species. *T. sericea*, *D. cinerea* and *D. mespiliformis* had relatively more seedlings and fewer mature plants in communal rangelands than in protected areas (Table 5 on page 117). *S. birrea* and *S. madagascariensis* had relatively more seedlings and a smaller representation of mature plants in protected areas. *D. melanoxylon*, in both protected areas and communal rangelands, had high numbers of seedlings relative to mature plants. *Combretum apiculatum* seedlings were found at a single protected area site and not in any communal rangeland sites, while mature plants were relatively abundant under both land uses. Similarly, *Combretum zeyheri* was relatively common in the mature plant assemblage, especially within protected areas and yet few seedlings were found. The relative abundance of woody plant species, as represented by seedlings, reproductively mature plants and the number of seedlings per mature plant, differed considerably with land use (seedlings: Spearman $R = 0.379$, $P = 0.16$; mature plants: Spearman $R = -0.098$, $P = 0.73$; seedlings:mature plants: Spearman $R = 0.036$, $P = 0.90$). *S. birrea* dominated the seedling community in protected areas, while *S. madagascariensis* seedlings were the most abundant in communal rangelands.

More seedlings (66%) in communal rangelands showed evidence of having been previously damaged than those in protected areas (51.4%) (Chi-square test statistic = 68.66, $P < 0.0001$). In communal rangelands, damage was largely from fire (26.5% of seedlings), followed by having been broken (16%) or partly eaten by livestock (10.9%) and insects (11.4%). The importance of factors impacting seedlings in protected areas was similar, with fire the most noticeable (22.2% of seedlings burnt) followed by having been broken (12.3%) or partly eaten by wild herbivores (9.8%) and insects (5.9%).

For all species there appeared to be a cohort of seedlings between 0.2 and 0.4 cm in stem diameter (Figure 4 on page 118). There was no significant difference between the overall stem diameter frequency distributions of seedlings sampled in communal rangelands and those sampled in protected areas (Figure 5 - page 119). For the five abundant species, seedlings less than 0.4 cm in stem diameter (most

Table 5: Number of seedlings sampled within protected areas and communal rangelands, contrasted with densities of (ha⁻¹) reproductively 'mature' woody plants for the same sites. Species are ranked according to their relative dominance in seedling and mature plant assemblages, and the ratio of their seedlings to reproductively mature plants (Chi-square results shown; bold P < 0.05).

SPECIES	seedlings				mature plants				seedlings:mature plants				Significant difference	
	protected	rank	communal	rank	protected	rank	communal	rank	protected	rank	communal	rank	Chi-square	P
<i>S. birrea</i>	149	1	108	2	17	8.5	67	2	8.765	1	1.612	6	34.60	< 0.0001
<i>T. sericea</i>	100	2	52	3	402	2	12	9	0.249	10	4.333	3	105.59	< 0.0001
<i>D. melanoxylon</i>	46	3	32	4	47	5	18	8	0.979	5	1.778	5	2.22	0.137
<i>S. madagascariensis</i>	39	4	9	10.5	6	15	24	6	6.500	2	0.375	12	25.92	< 0.0001
<i>C. apiculatum</i>	16	5	0	15	114	4	163	1	0.140	12	0.000	15	18.90	< 0.0001
<i>D. mespiliformis</i>	15	6	126	1	11	11	2	14	1.364	4	63.000	1	41.30	< 0.0001
<i>A. harveyi</i>	13	7	16	6.5	8	13.5	25	5	1.625	3	0.640	10	2.07	0.150
<i>C. collinum</i>	12	8	9	10.5	18	7	6	11.5	0.667	6	1.500	7	0.90	0.342
<i>D. cinerea</i>	11	9	16	6.5	161	3	1	15	0.068	14	16.000	2	90.19	< 0.0001
<i>P. africanum</i>	5	10	2	13.5	39	6	3	13	0.128	13	0.667	9	1.12	0.289
<i>L. capassa</i>	4	11	2	13.5	12	10	11	10	0.333	7	0.182	13	0.03	0.861
<i>C. hereroense</i>	3	12.5	12	9	17	8.5	6	11.5	0.176	11	2.000	4	8.53	0.0035
<i>L. schweinfurthii</i>	3	12.5	3	12	10	12	19	7	0.300	8	0.158	14	0.06	0.801
<i>C. zeyheri</i>	2	14.5	14	8	624	1	34	3	0.003	15	0.412	11	147.87	< 0.0001
<i>Z. mucronata</i>	2	14.5	25	5	8	13.5	27	4	0.250	9	0.926	8	1.67	0.197

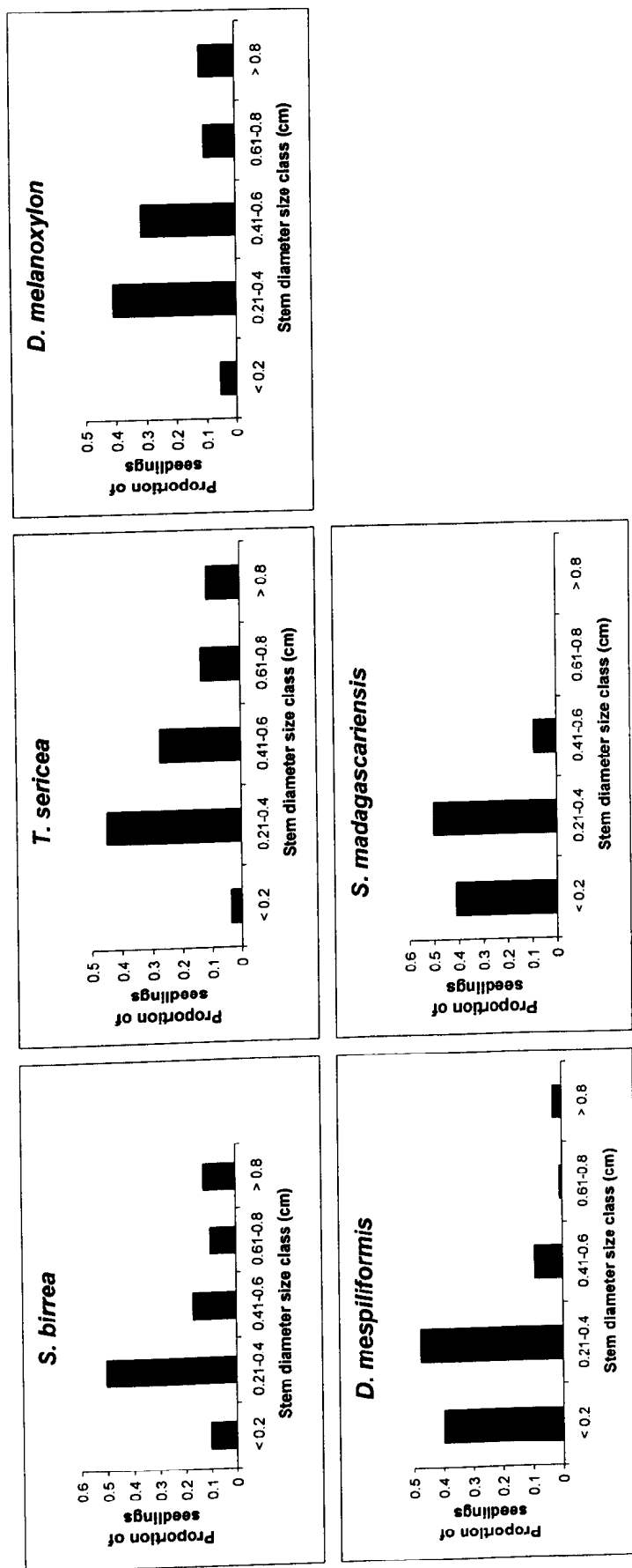


Figure 4. Stem diameter size frequency distributions for seedlings (protected area and communal rangeland site data combined) for the woody plant species with relatively large seedling samples.

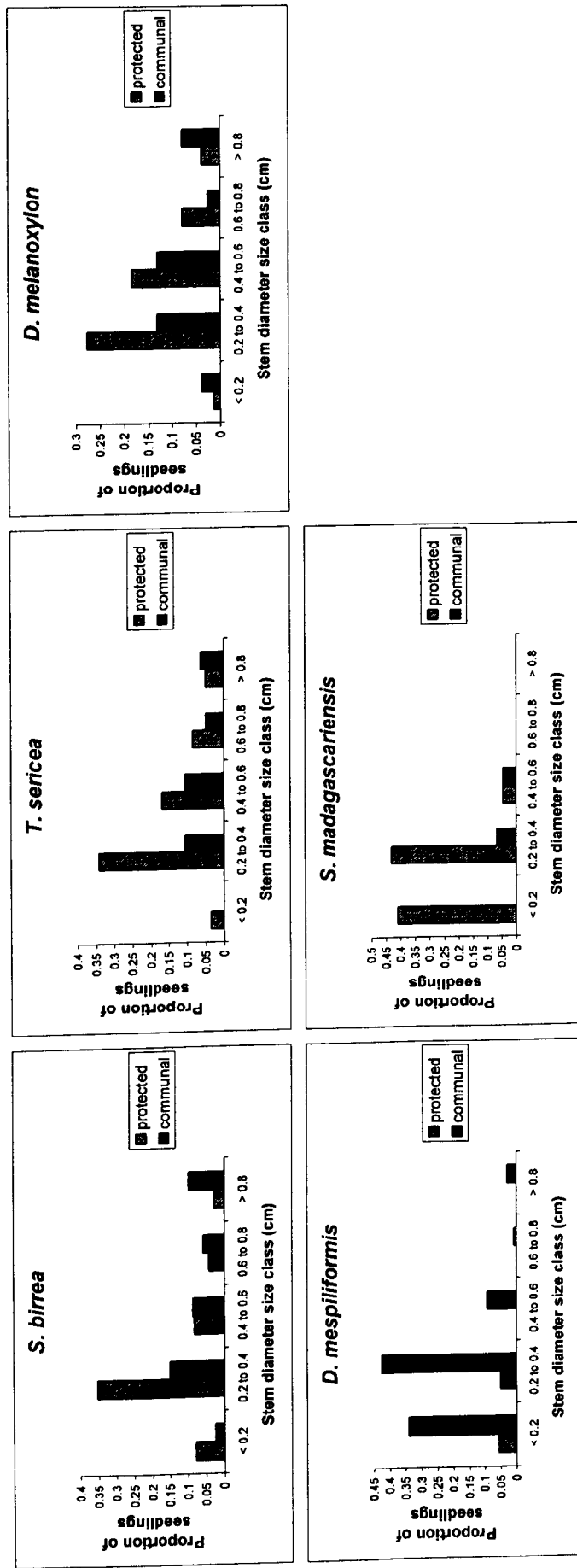


Figure 5. Stem diameter size frequency distributions contrasted for seedlings sampled in protected areas and communal rangelands, for the woody plant species with relatively large seedling samples.

pronounced for seedlings 0.2 to 0.4 cm in stem diameter) appeared to be more numerous in protected areas than in communal rangelands. There appeared to be slightly more seedlings larger than 0.8 cm in stem diameter in communal rangelands than in protected areas. *S. birrea* seedlings in communal rangelands were shorter in comparison to those in protected areas, larger in stem diameter and had more leaflets than those in protected areas (Table 6 on page 121). *T. sericea* seedlings were also larger in stem diameter in communal rangelands than in protected areas, with seedling height and leaflet number not differing significantly. In contrast, *S. madagascariensis* seedlings were taller in communal rangelands than in protected areas and had considerably more leaflets (the sample size of *S. madagascariensis* seedlings in communal lands was, however, small). The *D. mespiliformis* seedlings sampled in protected areas were taller than those in communal rangelands, larger in stem diameter and with more leaflets. *D. melanoxylon* seedling size did not differ significantly with land use. Grass height in communal rangelands was considerably shorter (14.34 ± 0.37 cm, $n = 436$) than in protected areas (21.67 ± 0.51 cm, $n = 528$) ($F_{1,808} = 3.85$, $P < 0.0001$) (in addition, refer to Appendix 3 for contrast of herbaceous cover by land use and along a gradient of rangeland utilisation).

4.3.2.2 Burnt and non-burnt site contrast

As expected, a high proportion (86.2%) of seedlings at the burnt site had evidence of fire damage whilst no fire scars were detected for seedlings at the non-burnt site. There were no significant difference between the seedling stem diameter distributions of the burnt and the non-burnt site (Figure 6 on page 122). Larger seedlings were more numerous in the burnt site than in the non-burnt site. Seedlings in the burnt site were generally shorter than those in the non-burnt site (the apical tip of many had been burnt back and they had since resprouted). *S. birrea* seedlings, which dominated the seedling assemblage, were shorter in the burnt site, larger in stem diameter and had more leaflets per unit height than those in the site that had not been burnt (Table 7 on page 123). Grass in the burnt area was shorter than in the non-burnt area (20.35 ± 0.7 cm and 32.59 ± 1.03 cm, respectively; $F_{1,304} = 96.16$, $P < 0.0001$).

Table 6. Seedling size (mean $\pm$ SE) contrasted for protected areas and communal rangelands, for the five woody plant species represented by abundant seedlings (ANOVA results shown, bold P < 0.05).

Species	Protected	n	Communal	n	F	P
<i>S. birrea</i>	height	215	12.23 $\pm$ 0.78 cm	108	$F_{1,321} = 25.26$	< 0.0001
	stem diameter		0.39 $\pm$ 0.02 cm		$F_{1,321} = 22.30$	< 0.0001
	leaflet number		22.09 $\pm$ 1.19		$F_{1,321} = 4.09$	0.04
	etiolation		2.68 $\pm$ 0.60		$F_{1,321} = 0.23$	0.63
<i>T. sericea</i>	height	131	13.68 $\pm$ 0.81 cm	50	$F_{1,179} = 2.75$	0.10
	stem diameter		0.44 $\pm$ 0.02 cm		$F_{1,179} = 12.63$	< 0.001
	leaflet number		21.92 $\pm$ 1.31		$F_{1,179} = 3.26$	0.07
	etiolation		3.14 $\pm$ 0.38		$F_{1,179} = 0.45$	0.51
<i>D. melanoxylon</i>	height	46	17.72 $\pm$ 1.4 cm	32	$F_{1,76} = 3.47$	0.07
	stem diameter		0.42 $\pm$ 0.03 cm		$F_{1,76} = 1.98$	0.16
	leaflet number		72.85 $\pm$ 7.73		$F_{1,76} = 3.27$	0.07
	etiolation		8.25 $\pm$ 2.67		$F_{1,76} = 1.11$	0.30
<i>S. madagascariensis</i>	height	50	13.26 $\pm$ 0.93 cm	6	$F_{1,54} = 10.45$	0.002
	stem diameter		0.25 $\pm$ 0.03 cm		$F_{1,54} = 2.95$	0.002
	leaflet number		30.64 $\pm$ 3.6		$F_{1,54} = 19.32$	< 0.0001
	etiolation		2.47 $\pm$ 0.29		$F_{1,54} = 3.05$	0.09
<i>D. mespiliformis</i>	height	43	15.58 $\pm$ 2.54 cm	125	$F_{1,166} = 12.68$	< 0.001
	stem diameter		0.35 $\pm$ 0.05 cm		$F_{1,166} = 7.51$	0.01
	leaflet number		10.77 $\pm$ 1.22		$F_{1,166} = 3.2$	0.04
	etiolation		0.89 $\pm$ 0.05		$F_{1,166} = 4.26$	0.08

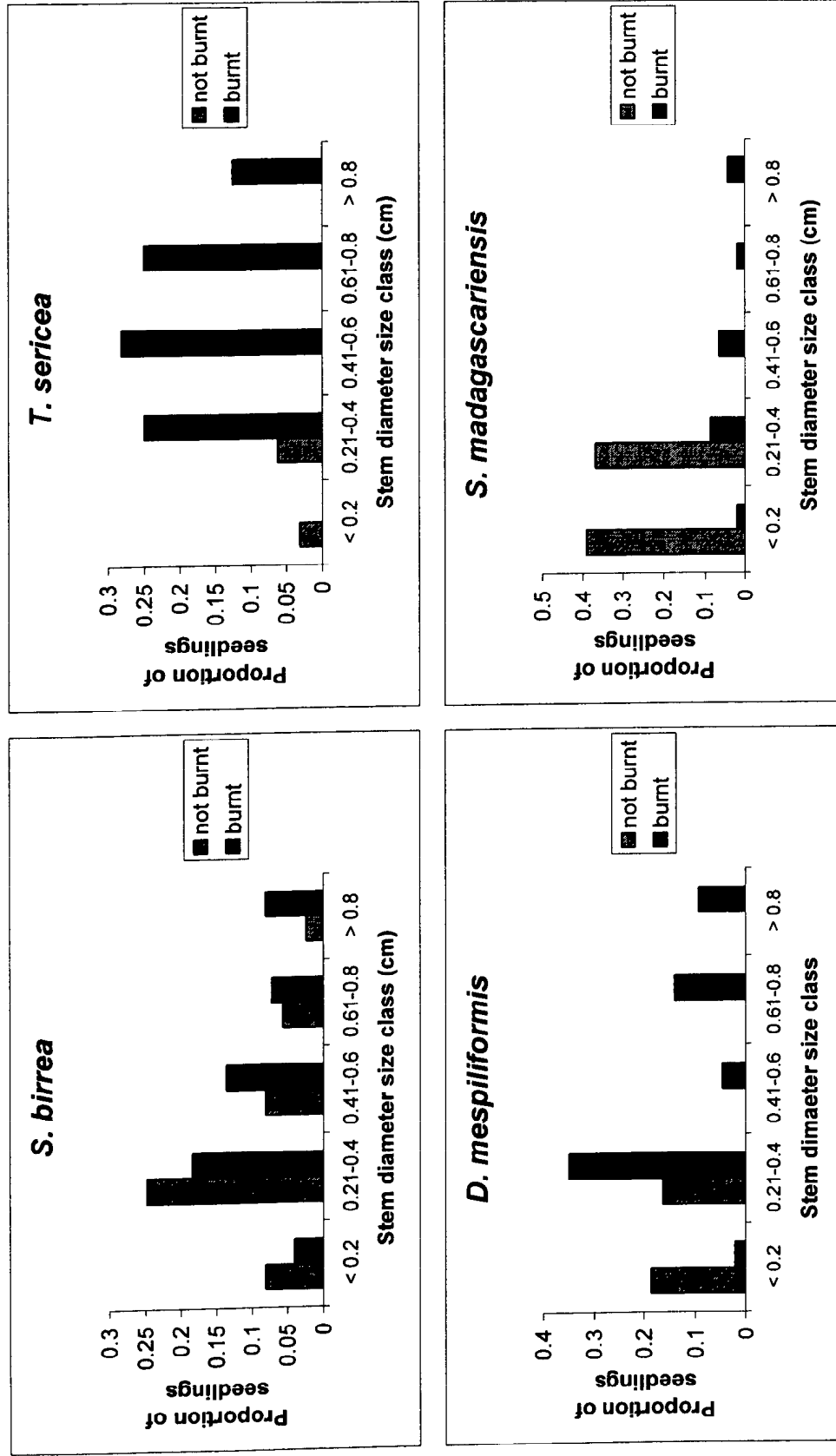


Figure 6. The stem diameter size frequency distribution of seedlings sampled in a recently burnt site contrasted with seedlings sampled in a non-burnt site within the same protected area, for the woody plant species with relatively large seedling samples.

Table 7. *Sclerocarya birrea* seedling size (mean $\pm$ SE) contrasted between a burnt and non-burnt site (ANOVA results shown, bold P < 0.05).

Seedling size	Burnt	n	Non-burnt	n	F _{1,125}	P
Height	14.23 $\pm$ 1.40 cm	66	22.84 $\pm$ 1.64 cm	61	16.11	0.0001
Stem diameter	0.52 $\pm$ 0.05 cm		0.34 $\pm$ 0.03 cm		8.39	0.005
Leaflet number	30.02 $\pm$ 2.31		24.79 $\pm$ 2.64		4.09	0.04
Etiolation	3.62 $\pm$ 0.53		1.21 $\pm$ 0.11		18.7	< 0.0001

4.3.2.3 *Sub-canopy and inter-canopy seedling microsites*

The majority (74.5%) of all recorded seedlings were found beneath the canopies of larger woody plants, with most species having a larger proportion of their seedlings beneath a canopy and only a few growing in inter-canopy areas (Table 8 on page 124). In contrast, *D. mespiliformis* seedlings only occurred beneath canopies, whilst more than half (57.4%) of *T. sericea* seedlings had established in inter-canopy areas. Relatively more *T. sericea* seedlings were growing in inter-canopy areas in communal lands than in protected areas (Chi-square = 7.27, P = 0.007, d.f. = 2): in protected areas 53% of seedlings grew in inter-canopy areas and 47% beneath canopies; in communal rangelands 77% of seedlings were found in inter-canopy areas and 23% in sub-canopy areas.

A quarter of *S. birrea* and *S. madagascariensis* seedlings and more than half the *T. sericea* seedlings growing beneath canopies, were growing beneath potential ‘parent’ plants, i.e. reproductively mature plants of the same species. Smaller proportions of the remaining seedlings were found beneath the canopies of other species. *D. melanoxylon* was anomalous in having more seedlings growing under *S. birrea* (36.2%) and *C. zeyheri* (19.0%) than under larger *D. melanoxylon* individuals (12.1%). For all species combined, the mean seedling ‘dispersal distance’ from the nearest reproductively mature adult was 19.9 $\pm$ 0.74 m (minimum distance = 0.5 m, maximum distance = 113 m; n = 768). Combretaceae seedlings were generally closer to potential parent plants, while the seedlings of *S. birrea* and *D. mespiliformis* were the furthest (Table 9 on page 124).

Table 8. The number of seedlings (mean $\pm$ SE) per woody species occurring beneath canopies and in inter-canopy areas contrasted for all sites, using two-sample t-tests assuming equal variances. Sample sizes of all species are given, including those with samples considered too small for statistical analysis (bold P < 0.05).

Species	Canopy	n	Inter-canopy	n	t statistic (10 d.f.)	P
<i>S. birrea</i>	32.0 $\pm$ 7.14	192	10.67 $\pm$ 3.09	64	2.47	0.010
<i>T. sericea</i>	9.83 $\pm$ 6.71	78	22.66 $\pm$ 14.84	105	-0.79	0.225
<i>D. melanoxylon</i>	9.67 $\pm$ 3.33	58	3.33 $\pm$ 1.63	20	1.71	0.059
<i>S. madagascariensis</i>	6.67 $\pm$ 5.13	48	0.83 $\pm$ 0.54	8	1.13	0.142
<i>D. mespiliformis</i>	23.33 $\pm$ 13.31	140	-	0	1.77	0.054
<i>D. cinerea</i>	-	20	-	7	-	-
<i>P. africanum</i>	-	7	-	3	-	-
<i>L. schweinfurthii</i>	-	6	-	1	-	-
<i>A. harveyi</i>	-	21	-	8	-	-
<i>L. capassa</i>	-	6	-	3	-	-
<i>Z. mucronata</i>	-	25	-	2	-	-
<i>C. collinum</i>	-	17	-	5	-	-
<i>C. hereroense</i>	-	8	-	7	-	-
<i>C. zeyheri</i>	-	8	-	8	-	-
<i>Pterocarpus rotundifolius</i>	-	1	-	1	-	-
<i>Cassine transvaalensis</i>	-	28	-	0	-	-
<i>Schotia brachypetalia</i>	-	21	-	1	-	-

Table 9. Distance (mean $\pm$ SE) of seedlings from the nearest potential 'parent', i.e. reproductively mature woody plant (n = sample size).

Species	Distance (m) of seedling from 'parent'	min Distance (m)	max Distance (m)	n
<i>S. birrea</i>	31.0 $\pm$ 1.49	1	113	266
<i>D. mespiliformis</i>	27.38 $\pm$ 2.37	1	100	66
<i>C. zeyheri</i>	20.07 $\pm$ 3.95	4	44	14
<i>P. africanum</i>	16.86 $\pm$ 3.49	10	35	7
<i>D. cinerea</i>	14.67 $\pm$ 3.15	2	55	18
<i>L. capassa</i>	13.57 $\pm$ 3.35	5	29	7
<i>L. capassa</i>	12.13 $\pm$ 2.26	1	53	32
<i>D. melanoxylon</i>	10.59 $\pm$ 1.86	0.5	29	16
<i>A. harveyi</i>	10.24 $\pm$ 1.08	1	27	33
<i>S. madagascariensis</i>	9.82 $\pm$ 0.66	0.5	85	163
<i>T. sericea</i>	9.27 $\pm$ 2.31	1	60	26
<i>Z. mucronata</i>	5.67 $\pm$ 1.00	1	18	19
<i>C. collinum</i>	4.33 $\pm$ 0.95	1	7	6
<i>C. apiculatum</i>	4.33 $\pm$ 0.95	4	5	6
<i>C. hereroense</i>				

S. birrea seedlings growing beneath canopies were smaller in stem diameter than those in inter-canopy areas and had fewer leaflets (Table 10 on page 126). *S. madagascariensis* seedlings growing beneath canopies were similarly smaller in diameter and had fewer leaflets than those in inter-canopy areas. In addition, they were significantly taller and more etiolated than those growing in direct sunlight. *D. melanoxylon* and *T. sericea* seedlings growing beneath canopies did not differ significantly in size from those in inter-canopy areas. There were no significant differences in the overall stem diameter distributions of seedlings occurring beneath canopies and those growing in direct sunlight (Figure 7 on page 127). Generalised linear model analyses established that seedlings of all species smaller than 0.4 cm in stem diameter size (and particularly those < 0.2 cm) were more closely associated with sub-canopy microsites than were larger seedlings ($F_{1,799} = 2.62$, $P = 0.02$) (Table 11 on page 129). There was no significant species by size class interaction, indicating that small seedlings are associated with sub-canopy microsites independent of species. The majority (90%) of seedlings were growing in microsites where grass covered less than 25% of the surrounding (1 m² quadrat) area, two thirds of which grew in microsites with < 10% grass cover. Seedling microsites beneath the canopies of larger woody plants were associated with a lower grass cover ($F_{1,804} = 7.49$, $P < 0.0001$) and more leaf litter ($F_{1,804} = 12.44$, $P < 0.0001$) than the microsites of those seedlings growing in inter-canopy areas. Soil 'moistness' did not differ between sub-canopy and inter-canopy microsites.

Grass height did not differ significantly between sub-canopy and inter-canopy areas. *Panicum maximum* was the most prevalent grass species beneath sub-canopies (74.1% of herbaceous cover). In inter-canopy areas, other species including *Hyperthelia dissoluta* (22.1%) and *Urochloa mosambicensis* (20.5%) were almost as common as *P. maximum* (35.7%). The same pattern was found when comparing the grass species with which seedlings were mostly associated in protected and communal rangeland sites: *P. maximum* was prevalent in protected areas (80.9%), whilst a combination of *P. maximum* (44.5%), *U. mosambicensis* (26.1%) and *H. dissoluta* (17.4%) surrounded seedlings in communal rangelands. More seedlings (70%) in inter-canopy areas than beneath

canopies (54%) had evidence of having been previously damaged, differing most noticeably in the proportion of seedlings that had been burnt or broken. Of those seedlings growing in inter-canopy areas that had been damaged, 30.9% had fire scars (as compared with 21.7% under canopies); 22.3% had been broken (11.1% under canopies); 3% (5.6% under canopies) and 4.3% (5.6% under canopies) had been partly eaten by game and livestock, respectively, and 6% (9% under canopies) had been partly eaten by insects.

Table 10. Seedling size and leaflet number (mean $\pm$ SE) contrasted for seedlings growing beneath canopies and in inter-canopy areas, for the woody plant species represented by abundant seedlings (ANOVA results shown, bold P < 0.05).

Species		Sub-canopy	n	Inter-canopy	n	F	P
<i>S. birrea</i>	height	16.67 $\pm$ 0.74 cm	243	15.79 $\pm$ 1.09 cm	80	F _{1,321} = 0.38	0.54
	stem diameter	0.40 $\pm$ 0.02 cm		0.70 $\pm$ 0.09 cm		F _{1,321} = 21.64	< 0.0001
	leaflet number	20.66 $\pm$ 0.89		32.46 $\pm$ 3.05		F _{1,321} = 25.53	< 0.0001
	etiolation	2.69 $\pm$ 0.53		3.21 $\pm$ 0.45		F _{1,321} = 0.29	0.59
<i>T. sericea</i>	height	14.47 $\pm$ 1.19 cm	78	11.82 $\pm$ 1.95 cm	105	F _{1,181} = 3.74	0.06
	stem diameter	0.48 $\pm$ 0.04		0.48 $\pm$ 0.03		F _{1,181} = 0.01	0.97
	leaflet number	21.62 $\pm$ 1.74		24.7 $\pm$ 1.34		F _{1,181} = 2.02	0.16
	etiolation	2.67 $\pm$ 0.37		3.7 $\pm$ 0.45		F _{1,181} = 2.77	0.10
<i>D. melanoxylon</i>	height	16.29 $\pm$ 1.23 cm	58	15.57 $\pm$ 2.09 cm	20	F _{1,76} = 0.09	0.76
	stem diameter	0.46 $\pm$ 0.04 cm		0.48 $\pm$ 0.11 cm		F _{1,76} = 0.07	0.79
	leaflet number	63.07 $\pm$ 6.6		70.2 $\pm$ 8.42		F _{1,76} = 0.34	0.56
	etiolation	8.12 $\pm$ 2.29		31.02 $\pm$ 24.73		F _{1,76} = 2.37	0.13
<i>S. madagascariensis</i>	height	14.34 $\pm$ 1.08 cm	48	13.88 $\pm$ 2.31 cm	8	F _{1,54} = 10.45	0.002
	stem diameter	0.23 $\pm$ 0.02 cm		0.45 $\pm$ 0.13 cm		F _{1,43} = 8.14	0.006
	leaflet number	31.58 $\pm$ 3.43		61.5 $\pm$ 16.6		F _{1,54} = 7.88	0.007
	etiolation	2.38 $\pm$ 0.26		4.20 $\pm$ 1.14		F _{1,43} = 5.51	0.02

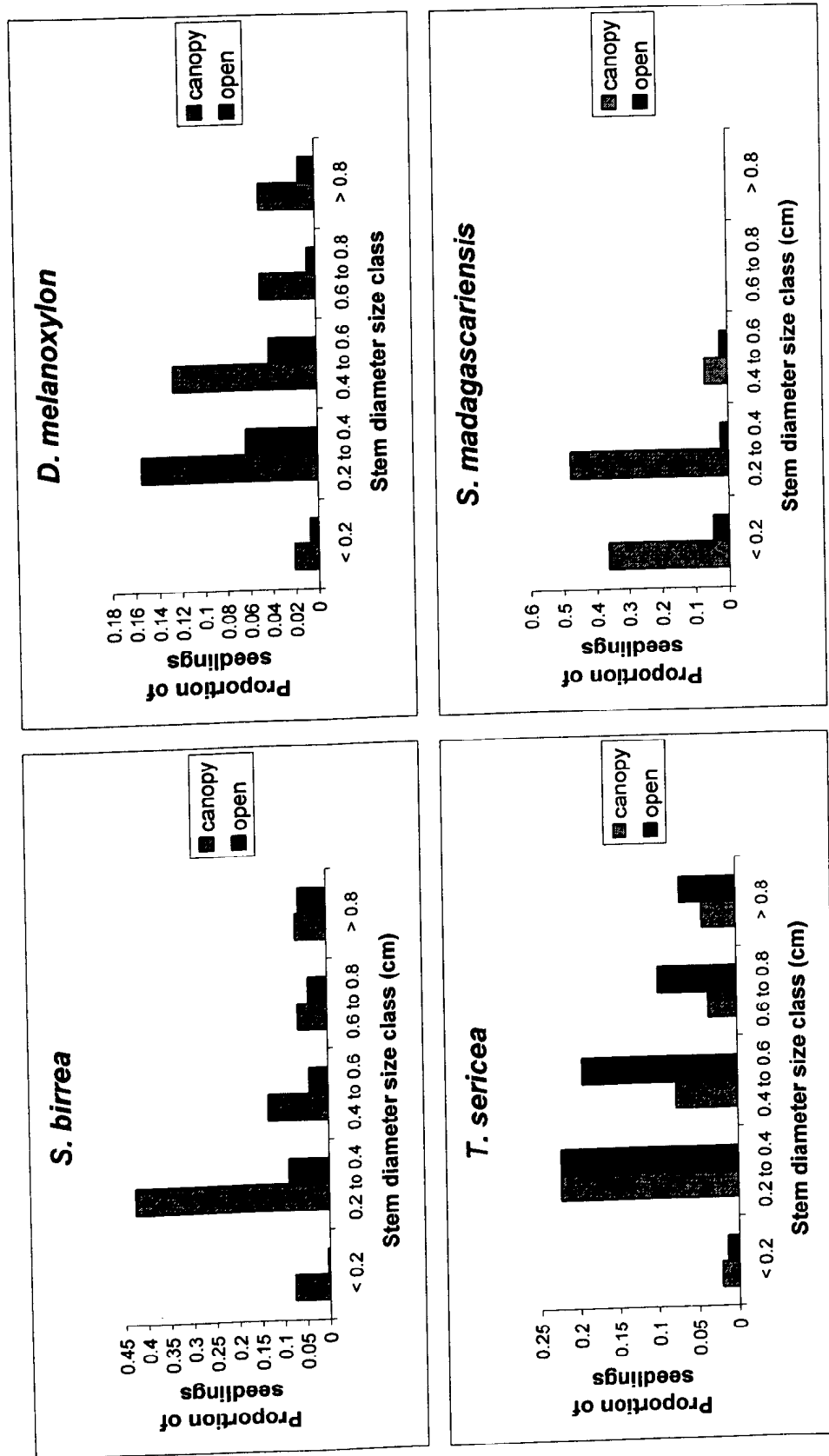


Figure 7. Stem diameter size frequency distributions contrasted for seedlings growing beneath the canopies of other woody plants and those growing in inter-canopy areas, for the woody plant species with relatively large seedling samples.

Table 11. Generalised linear model analysis of the association of seedlings (by species and stem diameter size class) with sub-canopy environments and seedling microsite characteristics compared for sub-canopy and inter-canopy areas (G^2 is the change in deviance and Δ d.f. is the change in degrees of freedom resulting from removal of a parameter, a binomial error distribution and logit link function were used; bold P < 0.05).

	Model Term	F	P	G^2	Δ d.f.
Seedling association <i>Species x Size Class</i>	Species : Seedling Size Class	1.31 (799)	0.16	21.52	20
	Species	48.19 (799)	< 0.0001	153.61	4
	<i>D. melanoxylon</i> : 0.74 $\pm$ 0.26				
	<i>S. birrea</i> : 0.75 $\pm$ 0.29				
	<i>S. madagascariensis</i> : 0.86 $\pm$ 0.46				
	<i>D. mespiliformis</i> : 1.0 $\pm$ 0				
	<i>T. sericea</i> : 0.43 $\pm$ 0.30				
	Seedling Size Class	2.62 (799)	0.02	10.43	5
	< 0.2 cm (SC 1): 0.90 $\pm$ 0.3				
	0.2 - 0.4 cm (SC 2): 0.78 $\pm$ 0.3				
Sub-canopy characteristics	Grass Cover + Leaf Litter + Soil	7.49 (804)	< 0.0001	29.73	4
	Grass Cover	12.44 (802)	< 0.0001	24.59	2
	Leaf Litter	2.17 (801)	0.14	29.73	4
	Soil				

4.4 DISCUSSION

4.4.1 The importance of grass cover

Together, the experimental findings of this study and the field description of seedling microsites provide evidence of the importance of grass cover in limiting, but not preventing, seedling establishment. There was a reduced emergence of *Strychnos madagascariensis* seedlings in plots with live grass relative to plots in which grass had been killed and either left *in situ* or cleared. *Sclerocarya birrea* and *Terminalia sericea* similarly had a lower seedling emergence in plots with live grass, suggesting that the competitive effect of grass cover is ubiquitously experienced as negative by woody plant seedlings at least during the first couple of growing seasons. The influence of grass competition on seedling survival was reduced both during the first growing season, presumably as a result of the supplementary watering, and during the winter period when grass was dormant.

During the second growing season, when below-average rainfall was received, fewer seedlings survived in live grass plots than in plots cleared of grass. There was no support for a facilitative effect of grass cover, with seedling emergence and survival not differing for plots in which all grass had been cleared and for those in which dead grass remained *in situ*.

Seedlings in plots containing live grass appeared to experience more stress than seedlings in plots either cleared of grass or containing dead grass cover. These seedlings were relatively etiolated and lost a larger proportion of their leaflets during the dry winter period. Seedling mortality was highest during the winter period for all grass treatments, with smaller seedlings less likely to survive. With the exception of *S. madagascariensis*, the low survival of the other study species, suggests that the experimental conditions were probably too dry for their successful establishment.

Small seedlings (< 0.4 cm in stem diameter) occurred more frequently beneath the canopies of other woody plants than in inter-canopy areas, indicating that sub-canopy conditions are more favourable during the early seedling stages. Seedlings growing beneath canopies were, however, more etiolated than seedlings in inter-canopy areas. Seedlings growing in sub-canopy environments were associated with a relatively lower grass cover and the majority of seedling microsites contained little (< 10%) grass cover. However, the relative importance of grass cover and other factors associated with sub-canopy environments e.g. lower temperatures and less fluctuation in soil moisture, was not determined in this study.

4.4.2 Herbivory and its interaction with grass cover

Seedlings growing in plots accessible to rodents were less likely to survive through the winter period (47% of seedlings survived) than those in either plots protected from all herbivores (75%) or those open to both ungulates and rodents (73%). This seemingly confounding finding might, however, have an explanation. Other studies have documented how a reduction in small ungulate herbivory can

lead relatively rapidly to an increase in vegetation cover (Prins & van der Jeugd 1993, Augustine & McNaughton 2004) and in some instances this may have the effect of supporting higher densities of rodents which have been found to reduce seedling numbers (Gill & Marks 1991, Keesing 2000). Although no measurements were made during the experimental period, grass cover is likely to have been higher as a consequence of protection from ungulate herbivory and to have benefited from supplementary watering. This increased herbaceous cover may have provided protection to foraging rodents at a time when recently emerged seedlings were most vulnerable. Nursery-grown seedlings with large fleshy cotyledons showed a high incidence of mortality due to rodent predation (personal observations). Additionally, seedlings growing in the plots accessible to herbivores had considerably fewer leaflets than seedlings in protected plots. This difference in leaflet number was most pronounced during the winter period: seedlings had 63% and 58% fewer leaflets in plots accessible to rodents and plots accessible to ungulates and rodents, respectively, than plots protected from herbivores. Green-leaved seedlings were clearly visible against a backdrop of dull dry dormant grass and are likely to have been apparent to herbivores. Seedling height was reduced by herbivory by both rodents and ungulates. The effect of herbivory, both on seedling leaflet number and height, was contingent on the interaction between grass treatment and the level of protection from herbivory. Seedlings in plots with live grass that were accessible to rodents were shorter and had fewer leaflets than those that were growing in plots cleared of grass. In contrast, in plots open to both indigenous ungulates and rodents, seedlings in plots cleared of grass were shorter and less leafy than those surrounded by live grass. These results are presented with a note of caution, with the number of replicates for the herbivory treatments acknowledged to be insufficient for complete confidence in the conclusions drawn.

Panicum maximum, the grass species most prevalent in sub-canopy seedling microsites is highly palatable to livestock and indigenous ungulates. Seedlings growing beneath the canopies of other woody plants had more evidence of herbivory (by livestock, indigenous ungulates and insects) than seedlings growing in inter-canopy areas, both in communal rangelands and in protected areas.

Seedlings growing in inter-canopy areas had a relatively higher incidence of fire or trampling damage, and grass species composition was indicative of disturbance. The distribution of larger seedlings in inter-canopy areas suggests that these established during periods when there were favourable rainfall conditions, no fire and a temporary release from grazing/browsing pressure.

4.4.3 Seedling distribution

Although reproductively mature *S. birrea* individuals were more abundant in communal rangelands (Shackleton *et al.* 2003, Chapter 2) seedlings were relatively more numerous in protected areas, perhaps indicating that conditions were less favourable for their establishment in communal rangelands. *S. madagascariensis* had both more adult individuals and seedlings in communal rangelands. *S. madagascariensis* was overwhelmingly the experimental species with the largest number of emergent and surviving seedlings, appearing to be tolerant of relatively harsh conditions. Both seedlings and adult plants of the species known to be most heavily utilised, including *T. sericea* and *Dichrostachys cinerea* (Chapter 2), were relatively less dominant in communal rangelands than in protected areas. In contrast, reproductively mature individuals of species valued for the edible fruit they provide (*S. birrea* and *S. madagascariensis*) were proportionately more abundant in communal rangelands. Woody species that regenerate primarily by resprouting are expected to produce fewer seedlings than species that regenerate mainly from seedlings due to trade-offs in resource allocation (Pate *et al.* 1990, Kruger *et al.* 1997, Bond & Midgley 2001). Even so, some degree of seedling recruitment is needed to establish new populations (Auld 1995). The species with the largest numbers of seedlings are all considered to be 'seeders'. These species generally had larger fruits, many of which are eaten and dispersed by animals (and humans), often to considerable distances. *Combretum apiculatum* and *Combretum zeyheri*, in contrast appear to have little seedling recruitment. Those seedlings recorded were closer to parent plants. Perhaps their seeds, dispersed by wind, get quickly lodged in grass or on other obstructions close to the parent plant. *Dalbergia melanoxylon* was the only species potentially showing signs of allelopathy, with fewer seedlings growing beneath parent plants

and more beneath the canopies of other species. Perhaps their light wind-dispersed seeds just travel further.

The majority of seedlings of most species occurred beneath the canopy of another woody plant. However, species clearly had different shade tolerances. *Diospyros mespiliformis* seedlings appeared to only survive in sub-canopy environments, while *T. sericea* seedlings were anomalous in appearing to ‘prefer’ direct sunlight conditions, supporting the finding of Yeaton (1998). In communal rangelands in contrast to protected areas, a higher proportion of *T. sericea* seedlings occurred in inter-canopy areas than beneath canopies. The highest incidence of *T. sericea* seedlings was in the sites that had been most heavily utilised or disturbed. Its tolerance for direct sunlight appears to enable it to recruit readily in sites that have been disturbed.

4.4.4 Seedling assemblage composition

Seedling regeneration in both communal rangelands and protected areas was highly patchy and yet similar patterns in seedling population structure were found. There was clear evidence for all woody plant species of pulsed recruitment in the form of a ‘seedling cohort’, estimated to be about two years of age (stem diameter size 0.2 to 0.4 cm) and likely to have established following the exceptionally high 1999/2000 rainfall season. Communal rangelands had fewer small seedlings than did protected areas. In general, seedlings in communal rangelands and in open microsites were shorter, yet larger in stem diameter, than those in protected areas or beneath canopies. Height suppression by ungulates and fire may inhibit growth resulting in a persistent ‘seedling bank’. A higher number of larger seedlings in the burnt site and their near absence in the non-burnt site indicates that these were resilient to the recent fire, unlike smaller seedlings. The non-burnt site had probably been intensively burnt 4 or 5 years previously, killing these seedlings before they had fully established. There were differences associated with land use, in the relative dominance of both seedlings and woody plants considered reproductively mature, and in the ratio of seedlings to mature plants.

The seedling assemblage was dominated by *S. birrea*, *Diospyros mespiliformis* and *Terminalia sericea*. In discussion with groups of local inhabitants (during the study period), making use of Participatory Rural Appraisal (PRA) techniques, there was consensus that *S. birrea* and *D. mespiliformis* are the woody plant species with the most abundant seedlings. Seedling emergence was higher for the large-fruited species (*Strychnos madagascariensis*, *Sclerocarya birrea* and *Ziziphus mucronata*), used in the field experiment. Larger seed nutrient resources presumably provide these species with a 'boost' that sustained seedling survival under conditions unfavourable for those with fewer reserves.

4.4.5 Conclusion

The findings of this study provide clear evidence that herbaceous vegetation directly influences the emergence and early survival of woody plant seedlings. The experimental results, together with the assessment of the location and microsite characteristics of seedlings in the field, suggest that small seedlings are especially vulnerable to dessication and damage. In addition, grass cover affects seedling exposure to herbivory. Seedlings surrounded by grass were more vulnerable to rodent predation, presumably because of the protection provided during foraging. Evidence of ungulate herbivory was higher for seedlings growing beneath the canopies of other woody plants than those growing in inter-canopy areas. Herbaceous composition of sub-canopy microsites was dominated by grass species considered highly attractive to herbivores.

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CHAPTER 5

Comparative Resprouting Response of Savanna Woody Plant Species Following Harvesting: the Value of Persistence

(Forest Ecology and Management, in press)

Abstract

An understanding of the relative ability of favoured fuelwood species to resprout following harvesting is integral to designing strategies for sustainable woodland resource utilisation. Harvester preference for particular woody plant species and plant size was examined in a formerly protected area, severely harvested over a short period of time. The resprouting response of harvested plants was measured four months after harvesting, towards the end of the wet season. Although a large proportion of stems of the dominant species (*Terminalia sericea* and *Dichrostachys cinerea*) had been harvested, certain less common species were targeted (e.g. *Pterocarpus rotundifolius* and *Peltophorum africanum*). Harvested plants were mostly larger than 4 cm in stem diameter. Almost all harvested plants of all species resprouted. Harvesting response was compared using three measures: (i) number of resprout shoots; (ii) composite resprout shoot diameter; and (iii) 'resprouting vigour' (composite resprout shoot diameter relative to composite cut stem diameter). Species differed in whether resprout growth was channelled into many small resprout shoots or fewer large shoots. The species most highly favoured by harvesters produced relatively large resprout shoots. Plant stem diameter size was the most important determinant of resprout output. Shoot number and their composite diameter increased with increasing plant size while resprouting vigour decreased. Cut height, although not having a significant effect on resprout output, influenced the location of resprouting, with taller stumps having a higher proportion of resprout shoots originating from the stem than from the root crown. For all species, approximately a third of the resprout shoots of harvested plants had died during the four months following harvesting. Shoots originating from the stem had a higher dieback than those growing from the root crown. Resprout biomass production over the four month period was considerable, amounting to 989 kg (wet mass) ha⁻¹. An abundance of seedlings of the most common species may be a consequence of the woodland having been thinned through harvesting.

Keywords: coppice management; fuelwood harvesting; natural resource sustainability; savanna woodlands; seedlings; woody plant regeneration

5.1 INTRODUCTION

Between 60% and 70% of South Africa's poor reside in rural areas, largely within the savanna biome (Shackleton 2001). In the Bushbuckridge District, falling within the lowveld savanna, approximately 70% of the potentially economically active population are unemployed (Shackleton 2000). Within this context, natural resources contribute considerably to livelihoods, providing fuel and food security and supplementing incomes (Shackleton 1999). As elsewhere in Africa (Eberhard 1990, Hall 1994), the vast majority of rural households continue to rely on fuelwood for their primary energy source. In densely populated areas, pressures on savanna woodlands from local inhabitants are high and woodlands are increasingly threatened (Grossman & Gandar 1989, Geldenhuys 1997). Within the Bushbuckridge region, the demand for fuelwood is predicted to be unsustainable over the next few decades (Griffin *et al.* 1992, Banks *et al.* 1996, Dovie *et al.* 2002). Indeed, as much as 93% of current demand is not met by available deadwood and is harvested unsustainably as live wood (Shackleton & Shackleton 2000). Despite the significant contribution of savanna woodlands to meeting the national requirement for biomass energy, their management has been neglected (Geldenhuys 1997) and there is limited empirical knowledge to guide their sustainable utilisation (Shackleton 2000, Maze 2001).

Following the damage or removal of aboveground parts, many savanna woody plant species resprout vigorously from roots and stumps (Gandar 1984, Grundy 1995, Frost 1996, Shackleton 1997, 2000, Maze 2001). The terms 'coppicing' and 'resprouting' or 'sprouting' have been used interchangeably in the literature. For the purposes of this study, the term 'resprouting' is used to denote shoots growing from the stem or stem base/root crown of a plant following damage. Resprouting is integral to savanna woody plant persistence, particularly in environments where there is a strong likelihood of aboveground damage and during periods when conditions are unsuitable for seedling recruitment (Higgins *et al.* 2000, Bellingham & Sparrow 2000, Bond & Midgley 2001). The persistence of important fuelwood species and the continued local availability of fuelwood is at least partly dependent on the ability of woody plants to survive harvesting damage

and to produce harvestable resprout growth. Researchers have advocated rotational harvesting systems based on the feudal English woodland (coppice) management systems (Gandar 1984, Grundy 1995, Kennedy 1998, Shackleton 2001). With no clear institutional support, this practice has not gained momentum. Optimistically, the promulgation of the New National Forests Act of 1998 will in time provide this support (Shackleton *et al.* 2001). An understanding of woody plant recovery following damage and the key factors influencing resprout output is essential for developing strategies for the conservation and sustainable utilisation of these woodlands by the communities whose livelihoods depend upon them.

It is difficult to compare woody plant resprouting ability across species and life stages without the use of controlled experiments and few studies have done so. The current study was initiated in response to a unique opportunity to assess woody plant resprouting capacity, following the intensive harvesting of a previously protected woodland by local people over a short time period. Harvester preferences for particular species and plant size were determined and the relative resprouting response of harvested plants was assessed. Specific questions answered included:

1. Were harvesters selective of plant species and size in relation to their availability?
2. Following harvesting, do woody plant species differ in their resprouting response?
3. Is resprouting response influenced by the size of the cut plant or by the height at which it has been cut?

In addition, resprout biomass and the extent of resprout dieback were assessed, and regeneration by seedlings and root suckers following harvesting was determined.

5.2 METHODS

5.2.1 Study area and woodlands

The study site (a privately owned piece of land approximately 300 ha in size at an altitude of ca. 640 m) is situated within the Bushbuckridge region of South Africa's Limpopo Province (31° 03' E; 24° 33' S). Until the early 1980s it functioned as a cattle ranch, but has since been unused. There was no perceptible evidence of previous harvesting of the woodland. The R531 road leading east to the Orpen Gate of the Kruger National Park delimits the southern border. The road divides lands under communal tenure to the south (prior homeland areas of the previous Mhala-Mapulaneng region of Gazankulu and Lebowa) from protected areas (private- and state-owned) to the north. Land under communal tenure is largely used as rangeland for cattle and for the harvesting of natural resources, whilst protected areas are mostly managed for wildlife-related tourism (Pollard *et al.* 1999). Population densities in the region are in excess of 300 people km² and Acornhoek, the closest settlement to the study site (less than 2 km to the south), is the largest in the region.

The region is characterised by low rainfall (ca. 650 mm per annum in the west; ca. 550 mm per annum in the east), concentrated in the summer season (October to May). This is mainly in the form of convectional thundershowers (Shackleton 1997). Intra-seasonal drought is common with more prolonged drought occurring as often as every 3.5 years. Mean annual temperature is 22° C. Mean daily maxima are approximately 30° C in January and 23° C in July (Pollard *et al.* 1999).

The topography of the study region is gently undulating. Soils are underlain by granitic gneiss with local intrusions of gabbro. Vegetation is broadly classified as Mixed Lowveld Bushveld and is dominated by species of the Combretaceae (Van Rooyen & Bredenkamp 1996). Additionally, the marula *Sclerocarya birrea* and sickle bush *Dichrostachys cinerea* contribute considerably to woody biomass within the region (Shackleton 1997). There have been several decades of intensive utilisation of communal grazing lands resulting in an alteration of woodland



Top: View of the study area following intensive harvesting of woody plants: tree stumps and broken branches on the ground and little grass cover. A fire had burnt the area following data collection. The densely wooded adjacent protected area can be seen across the slope in the background.

Bottom right and left: Woody plants showing a strong resprouting response following harvesting: here the resprout shoots of a round leaved teak *Pterocarpus rotundifolius* (bottom left) originate primarily from the stem, while those of a silver clusterleaf *Terminalia sericea* (bottom right) originate primarily from the root crown.

structure described as “short sparse woodland” by Edwards’ (1983) physiognomic classification. Adjacent protected areas have considerably denser woody vegetation and are classified as “short bushland”.

5.2.2 Field data collection

Woody plants in the ‘harvested site’ were cut within a two week period, prior to the onset of the wet season in September 2002. Although harvesting was prohibited, a large quantity of wood was rapidly removed from the site despite threats of arrest from the authorities.

Measurements were made four months following harvesting, towards the end of the wet season in March 2003: Twelve transects (4 m x 100 m) spaced equidistantly, 100 m apart, were used to assess the extent of harvesting in relation to species composition and stem size. All woody stems within transects were assessed for:

- species;
- woody plant height;
- whether a seedling, root sucker or larger woody plant;
- the proportion of the woody plant harvested (following Walker’s (1976) 8-point ranking scale);
- height of the largest cut stem;
- diameters of cut stems, intact stems and resprout shoots;
- length of the longest resprout shoot;
- location of each resprout shoot (stem or root crown).

About 90 completely harvested plants of six common species (*Dichrostachys cinerea*, *Terminalia sericea*, *Pterocarpus rotundifolius*, *Combretum zeyheri*, *Combretum collinum* and *Strychnos madagascariensis*) were assessed for the number of resprout shoots and the diameters of both resprout shoots and cut stems. Selected plants represented a range of cut heights. For 30 completely harvested plants of each of five species (four of the above-mentioned species: *D. cinerea*; *T. sericea*; *P. rotundifolius* and *C. collinum* and an additional intensively harvested species, *Peltophorum africanum*), the ‘status’ of resprout shoots was noted (i.e. whether alive or dead) distinguishing between shoots originating

from the stem and the root crown. The length and location of the longest resprout shoot were recorded.

Stem diameter (for both cut and intact plants) was measured close to the ground or just above the basal swelling when one was present. For multi-stemmed plants, the diameters of all stems were measured. The diameters of cut stems were measured at the cut surface and resprout shoot diameters were measured as close as possible to their origin with the stem/root crown of the parent plant. The ground around small plants was excavated to distinguish between seedlings and root suckers.

5.2.3 Data analysis

Harvester preference, i.e. the frequency with which harvesters had selected particular woody plant species and size plants, in relation to the woody plant species and size range present, was assessed at the level of stems. Resource-users are more likely to select by stem according to desired use and specific attributes. In contrast, resprouting response was analysed at the level of the individual plant. Plant size and the proportion of the plant harvested (together with the extent of belowground stored biomass and history of damage or unfavourable conditions) will determine the availability of resources that can be directed into the resprouting response of each stem. For multi-stemmed plants, a composite stem diameter was determined by calculating the cross-sectional areas of all stems, summing them and using this aggregate stem area to calculate the effective stem diameter. Composite diameters of resprout shoots and cut stems were similarly calculated for each harvested plant.

5.2.3.1 *Harvester preference for woody plant species and size*

In defining the available harvestable component of species populations, stems smaller than 1 cm in diameter (composed of seedlings and root suckers) were excluded as very few of these had been harvested. The proportion of harvested to non-harvested stems of each species was calculated to gauge whether harvesters actively selected particular species. Stems were divided according to diameter into classes to examine harvester preferences for particular size stems (all species pooled). The stem size class distributions of each of the common species were similarly calculated and the proportion of each size

class harvested determined. The stem diameter size classes selected followed those used by Luoga *et al.* (2000a, 2000b, 2002):

- 0 to < 1 cm: ‘seedlings’ (non-damaged newly established individuals) or ‘resprouts’ (here root suckers) (originating from active buds on roots, usually following damage);
- 1 to < 4 cm: ‘saplings’;
- 4 to < 10 cm: ‘poles’;
- 10 to < 20 cm: ‘small reproductive trees’;
- ≥ 20 cm: ‘large reproductive trees’.

5.2.3.2 *Woody plant resprouting response*

For each species, the proportion of harvested plants not resprouting was determined. In assessing the resprouting response of plants following harvesting, only plants that had been completely harvested (i.e. all stems had been cut) were considered. Resprout output was determined in three ways for each harvested plant: (i) the number of resprout shoots; (ii) the composite resprout shoot diameter; and (iii) resprouting vigour, calculated as composite resprout shoot diameter divided by composite cut stem diameter. Only plants that had had all their stems cut were included in the analysis. A mean of each resprouting measure was determined for the plants falling within each size class. This analysis was not carried out for cut height as regression analyses (described below) found it to be less influential for resprouting response. Whether species differed significantly from one another in their resprouting response, as expressed by each resprouting measure, was assessed using an analysis of variance. Resprouting response data were positively skewed and therefore transformed ($\log_{10}$) prior to analysis.

Generalised linear regression model analyses were used to compare the relative importance of the measured variables in determining the observed resprouting response. A gamma reciprocal link function was used for continuous response data and a quasipoisson log link function for discrete (overdispersed) response data. The explanatory variables tested were species, the size (composite diameter) of the cut plant, the interaction between species and plant size, and the height at which the plant was cut. The measures of resprout output were the response variables. The analysis was carried out for all species together, and for each species individually, following Crawley (2002) and

using R freeware V1.7.1. Graphs were plotted of the observed and predicted resprouting response in relation to the important explanatory variables.

5.2.3.3 *Resprout dieback*

To examine whether there were patterns in resprout shoot dieback, the proportion of resprout shoots that had died in relationship to total shoot number, together with their location on the plant, was assessed. An analysis of variance tested for species differences in the proportion of resprout shoots surviving. Chi-square tests (with Yates correction) determined whether resprout shoot survival was associated with origin (stem/root crown). Simple regressions determined whether resprout shoot persistence depended on plant size (composite cut stem diameter) or cut height.

5.2.3.4 *Resprout biomass and regeneration*

Basal stem diameters of intact and cut woody plants were used to calculate and contrast the woody biomass of the harvested site prior to and following harvesting, using a general allometric equation for broadleaved woody species (Netshiluvhi & Scholes 2002). The 'pre-harvest' biomass was composed of all woody plants of a diameter size larger than 1 cm, together with an estimate of the deadwood that had been available at the time of harvesting (Shackleton 1997). Plants less than 1 cm in diameter were considered to be seedlings and root suckers that had grown during the months following harvesting. The 'post-harvest' biomass included the biomass of intact woody plants, the biomass remaining in tree stumps of harvested woody plants, and new growth since harvesting by resprouting or newly emerging seedlings and root suckers. An estimate was made of the biomass of an 'average' tree, prior to and after harvesting, i.e. the remaining tree stump and resprout growth.

For the most common species sampled in the harvested site, the proportions of seedlings and root suckers forming the 0 to < 1 cm diameter size class were determined. Resprout shoots from the root crown or stem of a harvested plant were not included.

5.3 RESULTS

An area of 0.48 ha was sampled within which 972 plants comprising 4665 stems of 38 species were measured (Appendix 7). This translates into a density of 2025 plants ha⁻¹ or 9719 stems ha⁻¹. The most common species were *Dichrostachys cinerea*, *Terminalia sericea*, *Strychnos spinosa*, *Combretum zeyheri*, *Senna petersiana* and *Strychnos madagascariensis*. Excluding stems smaller than 1 cm in diameter, woody plant density was 801 plants ha⁻¹ and the most common species were *T. sericea* and *D. cinerea*, *S. spinosa*, *Pterocarpus rotundifolius*, *C. zeyheri* and *Combretum collinum*. Slightly more than 40% of the sampled plants were single-stemmed.

Within the area sampled, 62.1% of stems larger than 1 cm in diameter had been cut. Most harvested plants (93.6%) had had all their stems cut. Mean cut height was 0.7 m (SD = ± 0.53 m; n = 513). There was a significant difference in the height at which species had been cut ($F_{5, 507} = 6.73$, $p < 0.0001$; ANOVA), with *P. rotundifolius* the species with the highest mean cut height of 0.89 m (SD = ± 0.63 m; n = 103) and *S. madagascariensis* plants cut the lowest with a mean cut height of 0.52 m (SD = ± 0.4 m; n = 89). The height at which a plant was cut correlated with the mean plant height of the species (ANOVA: $F_{5, 572} = 19.4$; $P < 0.0001$), with *P. rotundifolius* having the tallest plants (mean height = 2.38 m; SD = ± 1.8 m; n = 47) and *S. madagascariensis* the shortest plants (mean height = 0.6 m; SD = ± 1.29 m; n = 59).

5.3.1 Harvester preference for woody plant species and size

The species that had been most heavily harvested were *Peltophorum africanum* (100% of stems larger than 1 cm had been cut), *P. rotundifolius* (98.2% harvested) and *S. madagascariensis* (88.2% harvested) (Figure 1 on page 150). The most abundant species, *T. sericea*, *C. zeyheri*, *C. collinum* and *D. cinerea*, had also been heavily harvested (82.5%, 75%, 71.4% and 45%, respectively, of stems larger than 1 cm in diameter had been cut). Prior to harvesting, more than half (57.3%) of all stems present in the study area had a diameter of less than 1 cm and 79.4% of all stems were smaller than 4 cm in stem diameter. Only 7.2% of stems in the 0-1 cm size category and 45.4% of stems in the 1-4 cm size category had been cut. Harvesters selected stems with diameters greater than 4 cm, i.e. falling within the 4-10 cm (82.6% harvested) and 10-20 cm size categories

(83.3% harvested). Few stems (0.01%) had a diameter size larger than 20 cm and these largely (88.9%) remained intact.

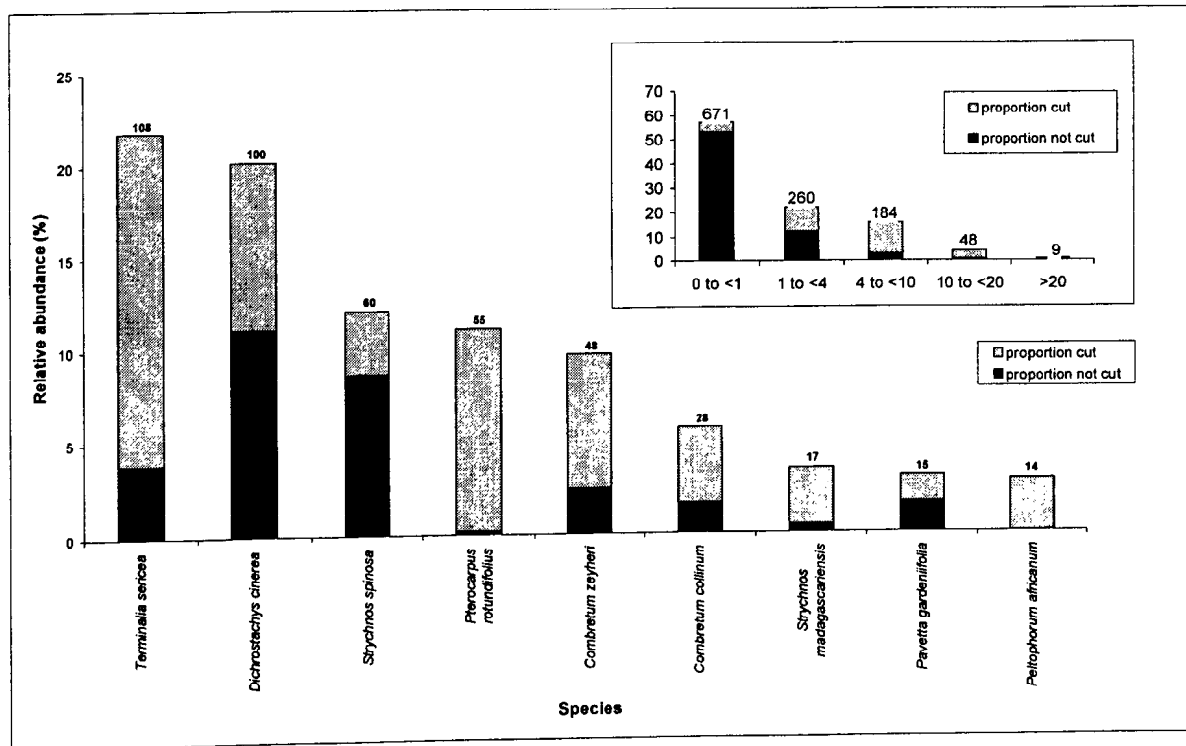


Figure 1. Relative stem abundance of woody plant species within the study site. The proportion of stems of each species harvested is represented. The number of stems is shown above the bars. Inset shows the proportion of each stem diameter size class harvested for all species combined.

The majority of stems larger than 4 cm in diameter of the most common species, *T. sericea*, *D. cinerea*, *P. rotundifolius*, *C. collinum* and *C. zeyheri*, had been harvested (Figure 2 on page 151). Despite *S. madagascariensis* stems being mostly less than 4 cm in diameter, a large proportion of them had been harvested. In contrast, *S. spinosa* had been less harvested.

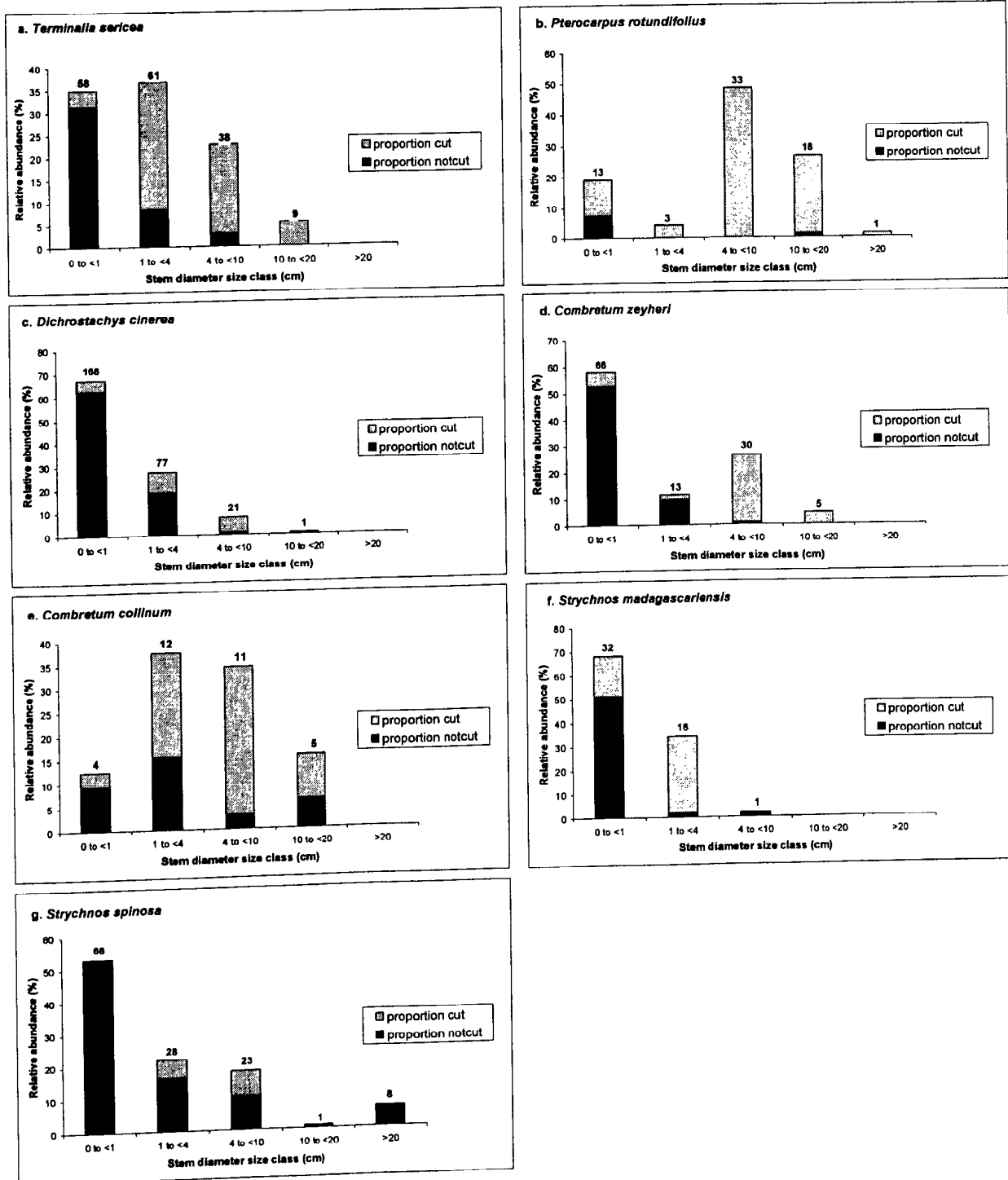


Figure 2. Stem diameter size distributions of a) *Terminalia sericea*; b) *Dichrostachys cinerea*; c) *Pterocarpus rotundifolius*; d) *Combretum zeyheri*; e) *Combretum collinum*; f) *Strychnos madagascariensis*; and g) *Strychnos spinosa*, with the proportion of each size class harvested shown.

5.3.2 Woody plant resprouting response

Almost all plants of all species resprouted (100% resprouting with the exception of *D. cinerea*: 93.3% of cut plants resprouted and *T. sericea*: 96.6% of cut plants resprouted). For each of the common species, resprout shoot number and composite resprout shoot diameter increased with increasing plant size, while resprouting vigour decreased. Within diameter size classes, individual plant resprouting response was quite variable (Appendix 8).

Species were found to differ significantly from one another in their resprouting response for all three measures of resprouting (resprout number: $F_{5,474} = 3.95$; $P = 0.002$; composite resprout diameter: $F_{5,474} = 3.67$; $P = 0.003$; resprouting vigour: $F_{5,474} = 8.50$; $P < 0.0001$). *D. cinerea* produced the highest number of resprout shoots per harvested plant with a relatively small composite diameter. In contrast, *P. rotundifolius* produced fewer resprout shoots per harvested plant with the largest composite resprout shoot diameter. *C. zeyheri* and *S. madagascariensis* had the highest composite resprout shoot diameter production relative to the size of the cut plant.

The generalised linear regression analysis for all species collectively found the number of resprout shoots produced per harvested plant to be influenced by plant size. The composite diameter of resprout shoots was influenced by plant size and to a far lesser extent by cut height. Resprouting vigour was influenced by plant size. In relationship to the other explanatory variables tested, species differences were found to be a significant determinant of resprout shoot number but not of composite resprout shoot diameter or resprouting vigour (Table 1 on pages 153-154).

In analysing the data of each species separately, plant size was the most important determinant of each of the three resprouting measures for the majority of species. Resprout shoot number was most strongly influenced by the size of the harvested plant with three exceptions, *D. cinerea*, *S. madagascariensis* and *C. zeyheri*, for which resprout shoot number did not differ significantly with plant size (Figure 3 on page 155). Plant size was again the most influential variable in determining the composite diameter of resprout shoots produced by a harvested plant, the exceptions being *D. cinerea* and

Table 1. Regression equations of best-fit generalised linear models for the most influential factors determining resprouting response (resprout shoot number; composite resprout shoot diameter and resprouting vigour, i.e. composite resprout shoot diameter relative to composite cut stem diameter) of entirely harvested plants of six woody plant species (parameter estimates $\pm$ SE).

Resprouting Response	Regression equations of best-fit models
Resprout shoot number	
<i>Species</i>	
<i>Dichrostachys cinerea</i>	$Y = e^{(2.09 \pm 0.08)}$
<i>Strychnos madagascariensis</i>	$Y = e^{(1.91 \pm 0.07)}$
<i>Combretum collinum</i>	$Y = e^{((1.71 \pm 0.02) + ((0.04 \pm 0.13) * \text{size}))}$
<i>Combretum zeyheri</i>	$Y = e^{(1.7 \pm 0.01)}$
<i>Terminalia sericea</i>	$Y = e^{((1.66 \pm 0.08) + ((0.03 \pm 0.01) * \text{size}))}$
<i>Pterocarpus rotundifolius</i>	$Y = e^{((1.49 \pm 0.07) + ((0.03 \pm 0.01) * \text{size}))}$
Composite resprout shoot diameter	
<i>Species</i>	
<i>Dichrostachys cinerea</i>	$Y = 1/((0.59 \pm 0.06) + ((-0.23 \pm 0.09) * \text{height}))$
<i>Strychnos madagascariensis</i>	$Y = 1/(0.55 \pm 0.04)$
<i>Combretum collinum</i>	$Y = 1/((0.57 \pm 0.07) + ((-0.02 \pm 0.01) * \text{size}))$
<i>Combretum zeyheri</i>	$Y = 1/((0.76 \pm 0.08) + ((-0.1 \pm 0.02) * \text{size}))$
<i>Terminalia sericea</i>	$Y = 1/((0.45 \pm 0.05) + ((-0.01 \pm 0.004) * \text{size}))$
<i>Pterocarpus rotundifolius</i>	$Y = 1/((0.44 \pm 0.07) + ((-0.01 \pm 0.003) * \text{size}))$
Resprouting vigour	
<i>Species</i>	
<i>Dichrostachys cinerea</i>	$Y = 1/((0.31 \pm 0.08) + ((0.36 \pm 0.03) * \text{size}))$
<i>Strychnos madagascariensis</i>	$Y = 1/((0.05 \pm 0.09) + ((0.51 \pm 0.09) * \text{size}))$
<i>Combretum collinum</i>	$Y = 1/((0.14 \pm 0.09) + ((0.33 \pm 0.05) * \text{size}))$
<i>Combretum zeyheri</i>	$Y = 1/((0.43 \pm 0.14) + ((0.24 \pm 0.008) * \text{size}))$
<i>Terminalia sericea</i>	$Y = 1/((0.32 \pm 0.07) + ((0.28 \pm 0.05) * \text{size}))$
<i>Pterocarpus rotundifolius</i>	$Y = 1/((0.37 \pm 0.17) + ((0.21 \pm 0.06) * \text{size}))$

For generalised linear regression models, the deviance is used to assess the goodness of fit of models to the data, and is contrasted to the null model in order to give an indication of the amount of data scatter explained. Models with the smallest deviance are the best fitting to the data. The relative importance of each explanatory variable is represented by the change in deviance resulting from its exclusion from the model. Variance in data increased with the mean: resprout number model uses a quasi-Poisson (log) link function, the response being transformed; resprout diameter and resprouting vigour models use a gamma (reciprocal) link function, with the inverse of the response. An F test with empirical scale parameter (instead of a chi-square test) was used to adjust for overdispersion.

Table 1 (cont). Significance testing of best-fit generalised linear models for the most influential factors determining resprouting response of entirely harvested plants of six woody plant species and for all species together (Height = height at which plant was cut; Size = composite cut stem diameter size; Significance (P): < 0.001 = highly significant (s*); < 0.05 = significant (s); > 0.05 = non-significant (ns); Dev. = change in deviance when a factor is excluded; Dev. Model = deviance explained by selected model; Dev. Null = deviance explained by null model, i.e. containing all variables and their interactions; degrees of freedom in parentheses).

Resprouting Response	Parameter significance			Dev. Model	Dev. Null
Resprout shoot number	Height P Dev.	Size P Dev.			
<i>Dichrostachys cinerea</i>	Ns 9.77	ns 4.44		-	122.4 (52)
<i>Strychnos</i>	Ns 4.77	ns 0.8		-	52.47 (49)
<i>madagascariensis</i>					
<i>Combretum collinum</i>	Ns 0.53	s 15.13		53.44 (35)	68.57 (36)
<i>Combretum zeyheri</i>	Ns 2.24	ns 0.18		-	35.82 (27)
<i>Terminalia sericea</i>	ns 0.57	s* 25.53		93.07 (72)	118.6 (73)
<i>Pterocarpus rotundifolius</i>	ns 0.01	s* 15.77		37.62 (53)	53.39 (54)
ALL species together	Height P Dev.	Size P Dev.	Species P Dev.	Species*Size P Dev.	
	ns 0.62	s* 60.28	s* 41.98	ns 5.58	390.96 (290) 498.08(296)
Composite resprout shoot diameter	Height P Dev.	Size P Dev.			
<i>Dichrostachys cinerea</i>	s 1.29	ns 0.19		12.86 (51)	14.15 (52)
<i>Strychnos</i>	ns 0.48	ns 0.51		-	14.79 (49)
<i>madagascariensis</i>					
<i>Combretum collinum</i>	ns 0.01	s* 5.12		11.72 (35)	16.83 (36)
<i>Combretum zeyheri</i>	ns 0.02	s* 4.07		6.68 (26)	10.75 (27)
<i>Terminalia sericea</i>	ns 0.64	s 3.31		40.71 (72)	44.02 (73)
<i>Pterocarpus rotundifolius</i>	ns 1.02	s 9.61		35.75 (53)	45.36 (54)
ALL species together	Height P Dev.	Size P Dev.	Species*Size P Dev.		
	s 0.62	s* 10.03	ns 5.58	127.82 (294)	155.39 (296)
Resprouting vigour	Height P Dev.	Size P Dev.			
<i>Dichrostachys cinerea</i>	ns 0.18	s* 27.44		10.62 (51)	38.06 (52)
<i>Strychnos</i>	ns 0.09	s* 19.97		14.69 (48)	34.65 (49)
<i>madagascariensis</i>					
<i>Combretum collinum</i>	ns 0.04	s* 31.38		15.54 (35)	46.93 (36)
<i>Combretum zeyheri</i>	ns 0.01	s 2.67		7.67 (26)	10.34 (27)
<i>Terminalia sericea</i>	ns 0.11	s* 44.97		35.05 (71)	80.02 (72)
<i>Pterocarpus rotundifolius</i>	ns 1.02	s* 24.99		38.24 (53)	63.23 (54)
ALL species together	Height P Dev.	Size P Dev.	Species P Dev.	Species*Size P Dev.	
	ns 0.42	s* 162.52	ns 2.45	ns 5.52	129.76 (294) 292.27 (295)

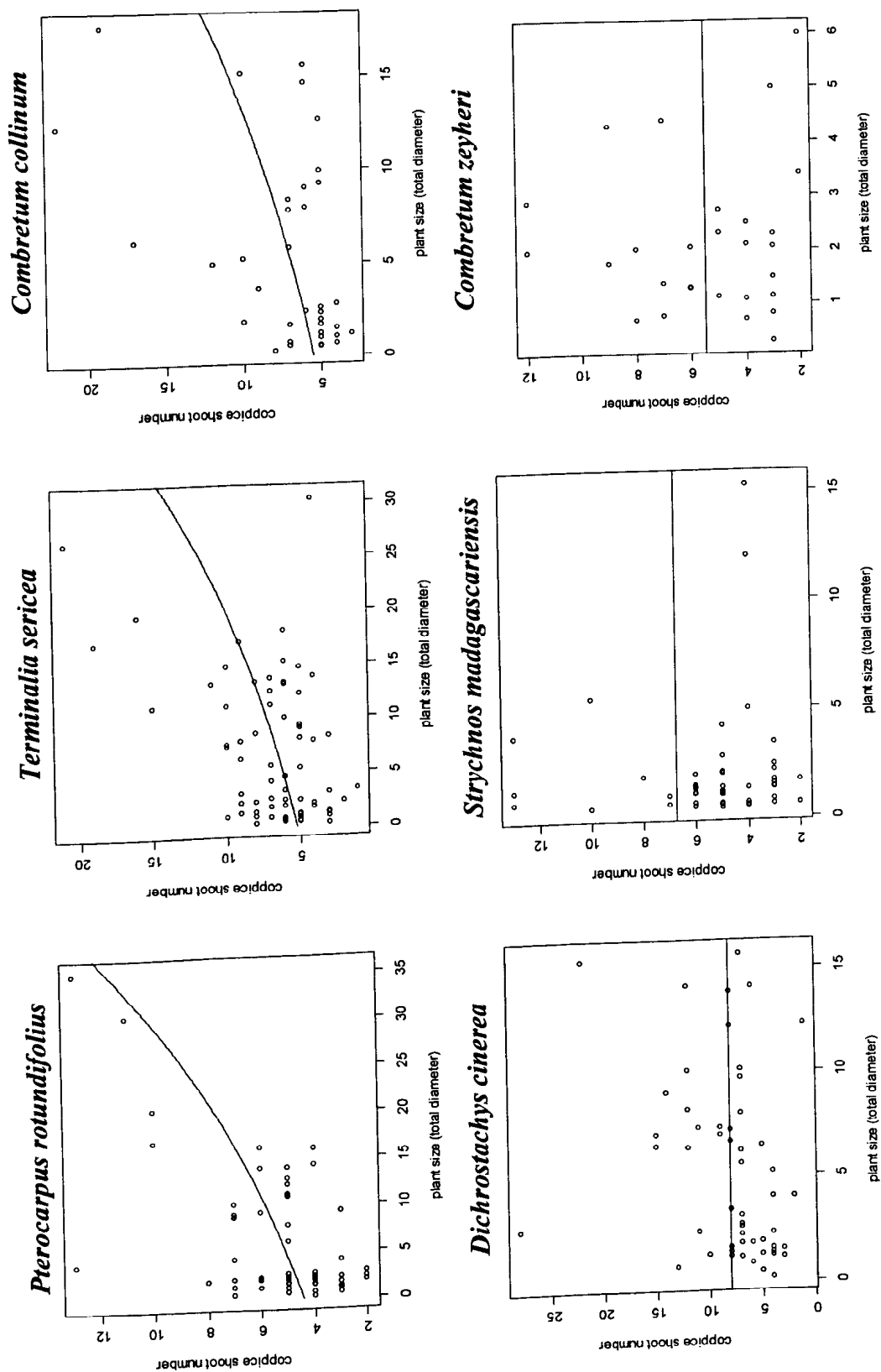


Figure 3. Resprout shoot number as influenced by plant size (composite stem diameter (cm)) of harvested plants of the six abundant woody plant species, with selected generalised linear regression model curves fitted.

S. madagascariensis for which increasing plant size did not result in a significant increase in composite resprout shoot diameter output (Figure 4 on page 157). Only for *D. cinerea* was composite resprout shoot diameter significantly influenced by the height at which plants were cut. Resprouting vigour was for all species negatively correlated to plant size, the composite diameter of resprout shoots decreasing relative to the composite diameter of cut stems with increasing plant size (Figure 5 on page 158).

When all species were considered together, more resprout shoots originated from the stem (55.2% of combined shoots; 95% CI = ± 0.054) of a harvested plant than from the root crown ($F_{1,304} = 7.24$; $p = 0.0075$; ANOVA). *P. rotundifolius* was the only species with a greater proportion of resprout shoots originating from the root crown (63.4%; 95% CI = ± 0.102) than from the stem, while *P. africanum* had the highest proportion of stem-originating resprout shoots (71.7%; 95% CI = ± 0.106). The height at which a plant was cut significantly influenced the location of resprouting: taller stumps were more likely to resprout from the stem, while resprouting from the root crown was more likely when the plant was cut lower down ($F_{1,151} = 39.37$; $p = 3.52 \times 10^{-9}$).

5.3.3 Resprout dieback

Four months following harvesting, 32.2% (95% CI = ± 0.02) of all measured resprout shoots had died. The proportion of shoots per harvested plant having died differed slightly between species ($F_{4,148} = 2.65$; $p = 0.0358$; ANOVA) with *D. cinerea* having the lowest resprout shoot dieback (27.3% of resprout shoots; SD = $\pm 16\%$) and *T. sericea* the highest (38.1% of resprout shoots; SD = $\pm 13\%$). For all species pooled, shoots originating from the root crown were more likely to be alive (70.3% of resprout shoots; SD = $\pm 22\%$) than those growing from the stem (62% of resprout shoots; SD = $\pm 27\%$) ($\chi^2_1 = 23.49$; $P < 0.0001$; $n = 3802$). This association was strongest for *D. cinerea* ($\chi^2_1 = 68.32$; $P < 0.0001$; $n = 908$), followed by *P. africanum* ($\chi^2_1 = 5.57$; $P = 0.018$; $n = 688$) and *T. sericea* ($\chi^2_1 = 4.53$; $P = 0.033$; $n = 519$). For *C. collinum*, the degree of resprout shoot dieback was similar for both the root crown and stem. Plant size and cut height

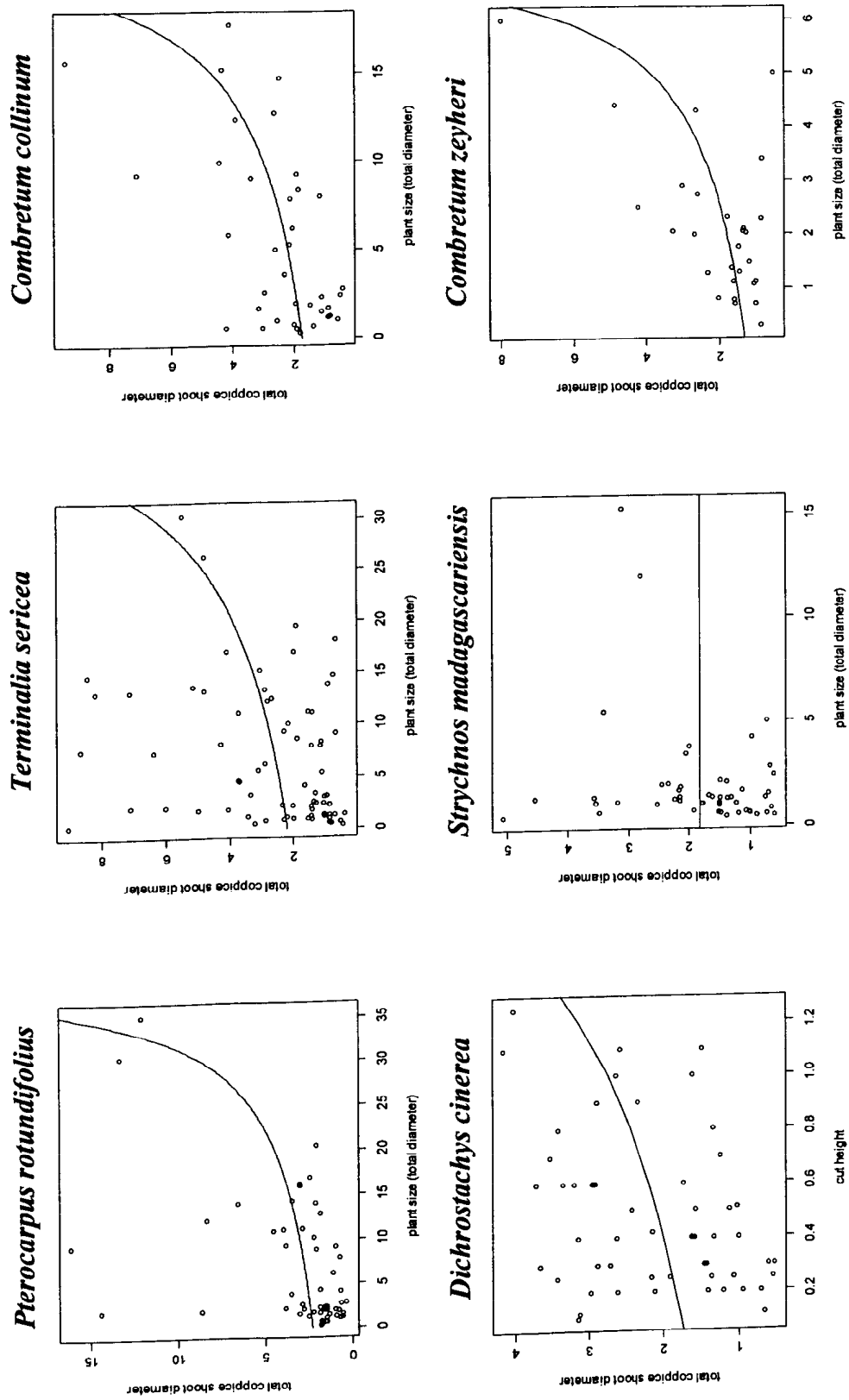


Figure 4. Composite resprout shoot diameter (cm) as influenced by plant size (composite stem diameter (cm)) of harvested plants of the six abundant woody plant species, with selected generalised linear regression model curves fitted. Note that for *D. cinerea*, cut height (m) was more important in explaining composite resprout shoot diameter than was plant size.

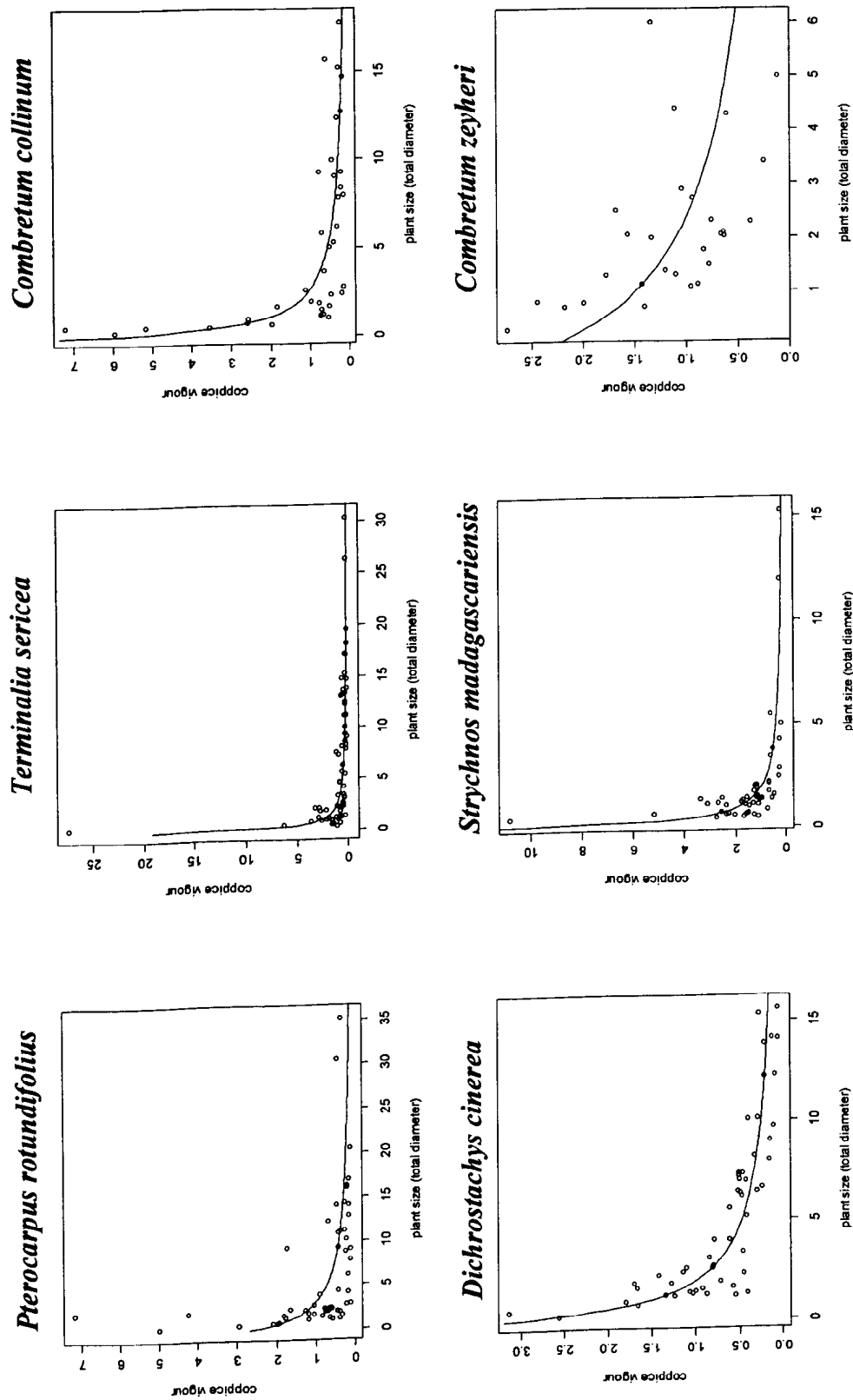


Figure 5. 'Resprouting vigour', i.e. composite resprout shoot diameter relative to composite cut stem diameter as influenced by plant size (composite stem diameter (cm)) of harvested plants of the six abundant woody plant species, with selected generalised linear regression model curves fitted.

did not influence resprout shoot survival. The longest resprout shoots originated from the stem for 63.4% of harvested plants. Just over half (53.6%) of the longest resprout shoots were alive, with the probability of being alive not significantly influenced by the origin of the shoot. The mean length of the longest resprout shoot for each species ranged from 1.13 m (SD = ± 0.5 m; n = 30) for *D. cinerea* to 2 m (SD = ± 0.63 m; n = 30) for *P. rotundifolius*.

5.3.4 Resprout biomass and regeneration

The 'pre-harvest' woody biomass of the study area was estimated to be 15 752 kg ha⁻¹ and the post-harvest biomass 15 008 kg ha⁻¹, of which 988.5 kg ha⁻¹ was resprout growth (Appendix 9). The biomass of an 'average' tree prior to being cut was 8.7 kg. After being cut, mean tree biomass was 7.1 kg of which 3.2 kg was resprout biomass. An estimated 268 kg ha⁻¹ harvestable deadwood could potentially be produced annually within the study area (using Shackleton's (1997) equation and the 'pre-harvest' standing wood biomass).

The proportion of seedlings to root suckers comprising the 0 to 1 cm diameter size class of both sampled *D. cinerea* and *T. sericea* populations was similar, with approximately two thirds seedlings (*D. cinerea*: 63.2%; *T. sericea*: 65.2%) and one third root suckers (*D. cinerea*: 36.8%; *T. sericea*: 34.8%). *C. collinum* had a greater proportion of seedlings (78.6%) relative to root suckers. In contrast, *S. spinosa* and *S. madagascariensis* had more root suckers than seedlings.

5.4 DISCUSSION

Although the most common species in the study site had been cut, harvesters favoured certain less abundant species, particularly *Peltophorum africanum* and *Pterocarpus rotundifolius*. All the species that had been harvested to a large extent are known to be favoured for fuelwood (Shackleton *et al.* 1998). *Dichrostachys cinerea*, having a relatively dense wood, also provides good fuelwood. That it had been less harvested in the study area is a reflection of a population dominated by small stems. Harvesting was forcefully terminated

following numerous threats of arrest by the authorities. The uncertainty of the situation is likely to have influenced the extent to which harvesters were selective, with both less time to search for the most desirable woody plants and to cut them. Woody plants were cut relatively high up with much wood biomass being left in the stumps. Harvesters clearly selected stems that were larger than 4 cm in diameter. Other studies have similarly reported these ‘pole’ and ‘small reproductive’ sized stems to be the most frequently harvested due to the ease of their transport and use for fuelwood and construction (Obiri *et al.* 2001, Luoga *et al.* 2004). The selective removal of woody plants in these size classes could severely impact woody plant demography by disrupting the recruitment of reproductively mature individuals.

There was no harvest-induced woody plant mortality during the four months following harvesting. All woody plant species and almost all plants of all sizes had resprouted. The few individuals that had not resprouted appeared to have been cut more recently. The height at which a plant was cut influenced the location of resprouting but did not significantly influence the number of resprout shoots. This is in contrast to the findings by Shackleton (2000) and Maze (2001) of increasing resprout shoot number with increasing cut height, attributed to a larger number of active buds with increase in stump surface area.

For all species, plant size was the most significant determinant of resprouting response. Both resprout shoot number and composite resprout shoot diameter increased with increasing plant size. However, relative to the cut stem diameter, composite resprout shoot diameter decreased with increasing plant size. All the study species were strong resprouters, differing in whether resprout growth was directed into many small or fewer large resprout shoots. Higgins *et al.* (2000) and Bond & Midgley (2001) hypothesised that species producing relatively few resprout shoots may indicate a “gulliver” life strategy, i.e. with plants growing rapidly to escape the zone of highest potential damage through investing resources into increasing the height of a few resprout shoots or the apical dominance of a single one. Perhaps *Combretum zeyheri*, with the lightest wood density of the study species and a relatively greater growth in resprout shoot length fits into this

life strategy category. In contrast, *D. cinerea* produced more resprout shoots and had less resprout shoot dieback, is dense-wooded and slow growing. *D. cinerea* may therefore follow Gignoux *et al.*'s (1997) "Stay and Resist" life strategy, having characteristics that enable it to survive within the zone of frequent damage. Given more time following harvesting, species differences in resprouting response might have been further pronounced.

Resprout growth contributed 6.6% to the total post-harvest biomass of the study site. Representing only four months of growth and under poor rainfall conditions, this resprout biomass of 989 kg (wet mass) ha⁻¹ is considerable. The estimated deadwood biomass present in the study site prior to harvesting was substantially less than the resprout biomass produced during this short time period. The mean diameter of resprout shoots was, however, still too small to be considered suitable for fuelwood. Shackleton (2001) found that resprout pruning of *T. sericea* resulted in a reduction in the time required before reharvesting, with remaining resprout shoots growing more rapidly than those of non-pruned plants. The large dieback of mostly stem-originating resprout shoots suggests that the preferential harvesting of these might be strategic and could result in increased growth rates of the remaining shoots.

Data collection occurred close to the end of a very poor wet season (only 41% of an average wet season's rainfall having been received), implying unfavourable conditions for seedling establishment. The large regenerative component composed to a great extent of seedlings is therefore unexpected and may be a response to the thinning of the woodland and the opening up of the canopy through harvesting. The seedlings of many species may, however, require the shade of larger woody plants to establish.

The findings of this study are in agreement with those of Shackleton (2000, 2001) and Kaschula (2003) that savanna woody plants are vigorous resprouters and that well-managed resprout production represents a valuable fuelwood resource. More extensive investigations into patterns of resprout growth of favoured fuelwood species are necessary, particularly in response to repeated harvesting. Sustainable

woodland management will require the controlled harvesting and subsequent resprout management of favoured species and plant size to prevent an undesirable change in woodland community composition and recruitment conditions and a loss of reproductive plants.

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CHAPTER 6

A Modelled Semi-Arid Savanna Landscape: Description of a Tool for Evaluating Strategies of Woody Plant Utilisation

Abstract

For rural households in South Africa, 70% of which reside within the savanna biome, natural resources contribute greatly to livelihoods (Shackleton 2001). As elsewhere in Africa, most continue to depend on wood as their primary source of fuel. High population densities, unemployment and extreme poverty place increasingly intense pressures on indigenous woodlands. With this motivation, a grid-based model was developed to further an understanding of the resilience of savanna woodlands in relation to their utilisation. The model simulates a disturbance (harvesting and livestock grazing/browsing) gradient outwards from a rural settlement and accounts for woody plant demographics and regeneration following harvesting, stochastic environmental variables (rainfall and fire) and seedling-grass competition. Three generic woody plant species representing different 'functional groups' are considered. Species differ in their desirability to harvesters, in their resprouting response following harvesting and in their reproductive output. The model projects spatial and temporal changes in the woodlands and resource availability, i.e. shifts in species composition, population structure, growth form and reproductive capacity, supporting an evaluation of alternative scenarios and strategies for their management. Although the model is based largely on data from the 'lowveld' savanna of South Africa, similar savanna systems and the dependency of rural households upon them, are characteristic of large areas of Africa and other developing countries. The flexibility of the model encourages its adaptation to effectively explore other questions and contexts, including the influence of socio-economic factors. In model formation, existing information is combined in a compact way and gaps in knowledge are apparent. This proved a useful exercise for synthesising present understanding of savanna woodland systems and for highlighting where the emphasis of future studies needs to be placed. The model concept and structure are described. An imminent publication will detail the model results.

Key-words: fuelwood harvesting, natural resource management, resprouting, seedlings, spatially explicit individual-based model, savanna woodlands, woody plant demography

6.1 INTRODUCTION

Savannas have long been exposed to and modified by the influence of humans, their management of fire and indigenous herbivores, their keeping of livestock and use of wood. Woody plant species show traits that indicate that they are to some extent 'tolerant' of disturbance: being long lived and maintaining belowground resources, they persist through unfavourable times, recover from damage by resprouting, reproduce and recruit episodically at times when conditions, primarily rainfall, are favourable. However, the degree to which savanna woodlands are being stressed is increasing in intensity, extent and duration. As human populations become more sedentary, grow in size, and in many cases experience extreme poverty, they depend heavily on natural resources (Erskine 1987, Grossman & Gandar 1989, Moss 1996). This is especially true in the South African context, where in the 1970s under apartheid's "Betterment and Villagisation" policy 'homelands' were created to which large numbers of black people were relocated having been removed from 'white-owned land'. With underdeveloped infrastructure and few local employment opportunities, livelihoods were and continue to be, highly reliant on the communal rangelands and woodlands surrounding settlements (Pollard *et al.* 1999; Niehaus *et al.* 2001; Dovie *et al.* 2002).

The effect of human use of communal rangelands is clearly visible in the distinct alterations in vegetation structure, species composition and biomass with distance from settlements, suggesting that vegetation patterns are related to spheres of disturbance associated with levels of resource harvesting and grazing (Shackleton *et al.* 1994, White 1999, Chapter 2). A loss of reproductively mature individuals would limit population recruitment, as would changes in the microsite conditions that are favourable for seedling establishment (Chapters 2 and 4). Height suppression of immature or (previously harvested) resprouting woody plants by browsing livestock could create a bottleneck in recruitment into the reproductively mature population. It is not clear what the long-term changes to these woodlands will be, whether they are reversible and the implications thereof. It is likely that there are certain plant functional types that would be more effective than others in

persisting in the face of intensive utilisation pressures. However, these may not be desirable for fuelwood? Also of interest is the relative importance of seedling recruitment and persistence through resprouting (Bond & Midgley 2001) for the regenerative capacity of different species and their endurance within disturbed savanna woodlands. Additionally, it is predicted that climate change and increasing carbon levels will promote conditions favourable for woody plant recruitment, perhaps favouring a different suite of species. There is an urgent need to manage these woodlands for the sustained availability of favoured fuelwood species. To do so requires an ecological understanding of the system, together with the ability to predict and examine the outcome of alternative scenarios or resource management strategies.

The empirical data collected in this study (and examined in Chapters 2 to 5), represent a fixed point in the lifetime of these savanna woodlands, a 'snapshot' in the midst of ecosystem change (Wiegand *et al.* 2000). To more completely understand and be able to predict the responses of savanna woody plant species to stresses that are intensifying both as a consequence of increasing utilisation pressures and environmental change, it is essential to consider change over longer time scales. Simulation modelling is a powerful tool, in this case enabling the exploration of savanna woodland change in species composition, population structures and woody plant growth form in space, and over time, and in identifying the most important drivers of this change. Supported by an empirical understanding, a model provides a 'experimental laboratory' for testing the response and resilience of woodlands and the species they contain under alternative conditions or scenarios of utilisation. A spatially explicit model is effective in describing the interactions between plants and their environment that are crucial to plant population dynamics. An individual-based modelling approach was considered appropriate as plants of different species and size differ in their growth rates and reproductive output, in their desirability to harvesters and their resprouting recovery following damage.

A description of the model, developed to examine woody plant demographics in the communal lands surrounding a settlement whose inhabitants depend on it for

fuelwood, follows. The model objectives were to (i) enhance understanding of the spatio-temporal dynamics and regenerative ability of semi-arid savanna woody plant vegetation, particularly in a context of wood harvesting; (ii) explore how alternative plant functional types endure in the face of disturbance; (iii) weight the relative importance of seedling recruitment and coppicing for species persistence; and (iv) formulate strategies for the sustainable utilisation of savanna woodlands.

Further development of the model, as a tool investigating strategies for savanna woodland sustainable utilisation and conservation, will follow. Strategies tested include situations where: (1) harvesters are selective of woody plant species and size and cut woody plants throughout the woodlands although their efforts are focused closer to the settlement (selective harvesting), (2) harvesters cut woody plants within a predetermined area, following which another area is harvested and the first area is protected while woody plants recover (rotational harvesting), (3) harvesters practise ‘coppice with standards’ management, i.e. the resprout shoots of previously harvested woody plants are managed and harvested (coppice harvesting). The term ‘standards’ refers to reproductively mature individuals, protected from harvesting to ensure sustained recruitment capacity.

In creating the woodland model, Einstein’s subtle modification of Occam’s razor was followed: “A model should be as simple as possible. But no simpler.” (Crawley 2002).

6.2 MODEL DEFINITION AND RATIONALE

6.2.1 Conceptual Definition

6.2.1.1 *A rural settlement and its communal lands*

The original concept for the model structure was based on the dynamics of savanna woodlands and communal rangelands surrounding a settlement in the Bushbuckridge region of South Africa’s northern Limpopo Province. The woodlands surrounding Thorndale have been extensively researched during the current study (Chapter 2). Other studies contribute additional information on

natural resource utilisation and the socio-economic context (Giannecchini 2001; Dovie *et al.* 2002). Thorndale is a remote settlement, bordering the Manyeleti National Park (31°28'E; 24°30'S). It has limited access to social infrastructure and can be described as a farming settlement. The population is estimated to be 450 persons from 71 households (with a mean of 6.28 ± 0.8 (SD) people per household). The mean annual consumption of fuelwood in the settlement has been estimated to be 4343 ± 333 (SD) kg per user household, with 96% of households depending on fuelwood for their primary fuel source. Limited agro-ecological potential, a growing human population, and scarce employment opportunities are a powerful combination undermining the prospects for sustainable resource use (Dovie *et al.* 2002). Many other settlements within the Bushbuckridge region have larger populations than Thorndale. In the communal lands surrounding these settlements, woodland resources have been more intensively and extensively used. The selling of fuelwood reflects a growing scarcity.

6.2.1.2 A gradient of resource utilisation

Empirical observations, by this and other studies (Liengme 1983, Shackleton *et al.* 1994), have documented the gradient of utilisation-related disturbances and associated vegetation patterns, extending outwards from settlements within savanna woodlands of the study area (Chapter 2). The model focuses on the impacts of fuelwood harvesting, livestock grazing/browsing and fire on the woodlands surrounding the settlement. Vegetation dynamics, including growth and recruitment, in semi-arid savanna ecosystems are largely 'event-driven' by stochastic and unpredictable rainfall. In this case there is a superimposed gradient of impact of selective harvesting of woody plants and livestock browsing. Livestock grazing determines grass biomass, influencing both seedling establishment (Chapter 4), and the incidence and intensity of fire and its impact on woody plants. The ability of stems to resprout following damage is a key life-history trait that promotes the persistence of savanna woody plants (Walter 1971; Bond & van Wilgen 1996; Gignoux *et al.* 1997; Trollope 1998, Bond & Midgley 2001) and the model simulates this recovery. The realism of the model results and ensuing predictions are assessed using empirical data collected in the woodlands

of communal rangelands and adjacent protected areas in the region surrounding this and other nearby settlements.

6.2.2 Operational Definition

The model is spatially explicit, grid-based and structured to depict a transect (3000 m by 100 m; 2122 x 71 cells) through the savanna woodland surrounding a settlement along a gradient of utilisation disturbance (Figure 1 on page 174). The transect length reflects the maximum distance that livestock venture from the settlement and that people harvest fuelwood by foot. Cell size (2 m^2 , with sides = $\sqrt{2}$) represents an average mature woody plant canopy. The model simulates the processes that influence woody plant species, from individual woody plants to the populations that they constitute. Biological information is described by equations and rules, permitting the inclusion of both quantitative and qualitative knowledge. The model implicitly considers competition by excluding the co-occurrence of two plants in a single cell: competition between seedlings ensures that there is no more than a single individual per cell. Grass biomass, dependent on rainfall and grazing intensity by livestock influences seedling emergence and initial survival. Competition between individuals of neighbouring cells is not explicitly modelled, instead the densities of established individuals (based on empirical data) are considered to reflect the outcome of density-dependency. Temporal dynamics are modelled in annual time steps. Within each annual time step woody plants grow and reproduce in response to stochastic rainfall, may be harvested, browsed or burnt, following which they may recover or die (Figure 2 on page 175). The model provides information at any time step, on the distance of each grid cell from the settlement and associated probability of disturbance, together with woody plant presence, identity, and grass cover. In each time step the model also describes whether a woody plant is resprouting or not, and if resprouting, the length of 'recovery time' since it was harvested. Changes in species abundance, spatial distribution, population structure and regenerative capacity are assessed over time.

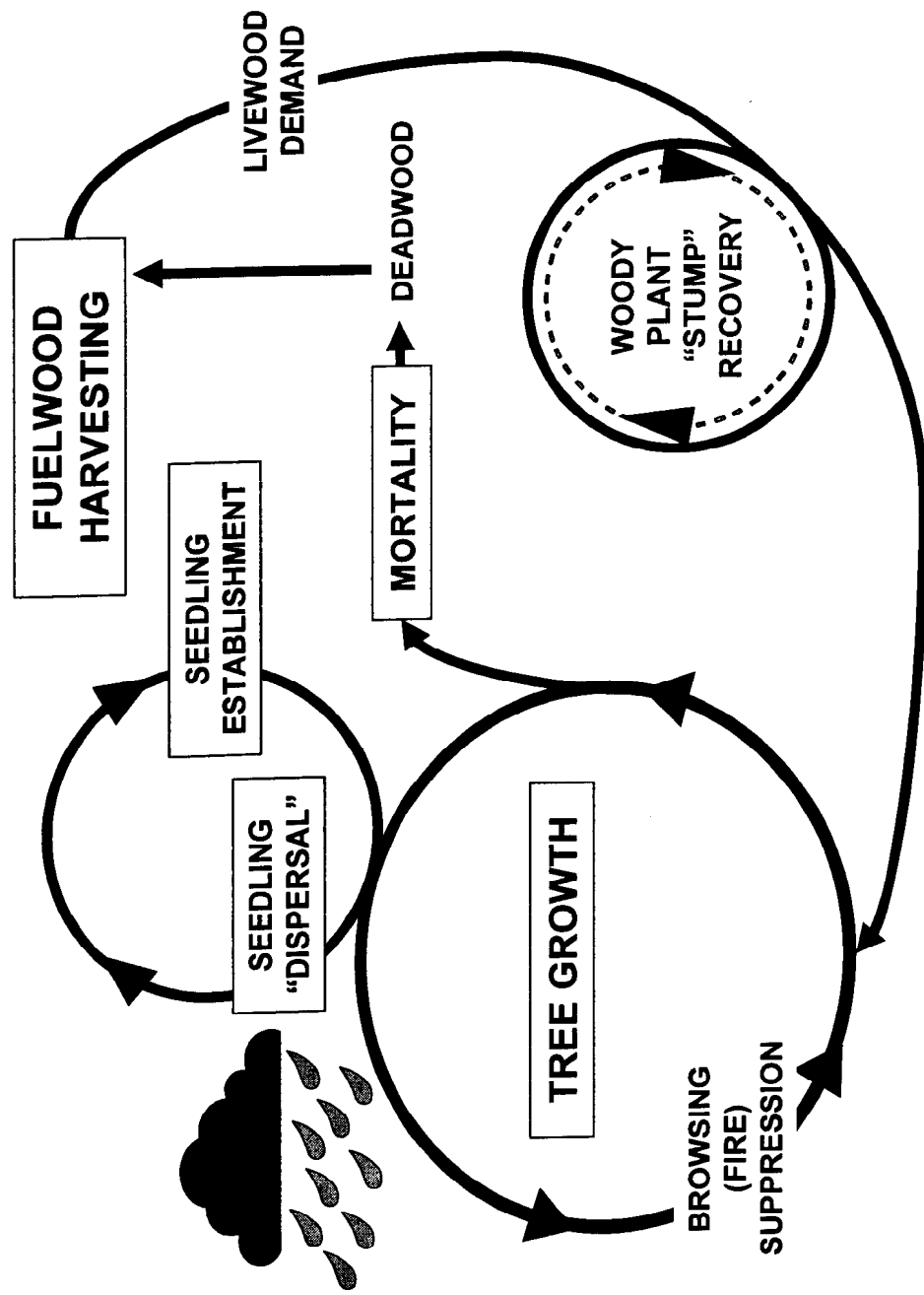


Figure 1. Conceptual diagram of the modelled drivers of woody plant growth and demography, including the harvesting of live wood and subsequent 'stump' resprouting recovery.

"DISTURBANCE" GRADIENT

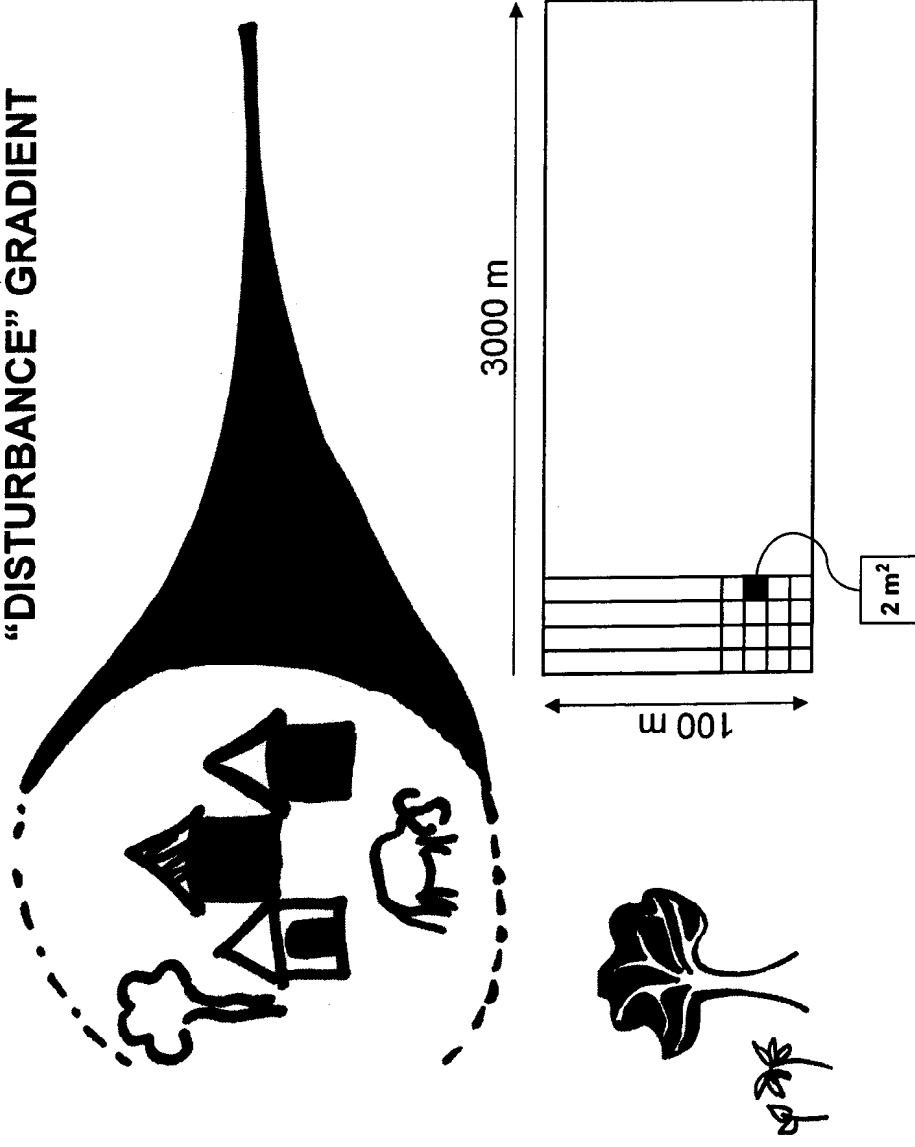


Figure 2. Diagram of the disturbance gradient and modelled transect outward from a settlement. Both harvesting and cattle grazing/browsing intensity are highest in the vicinity of the settlement than further away. Competition between seedlings ensures that each grid cell contains only a single woody plant.

The functions used to simulate the ecological processes (introduced in Figure 2 on page 175) are described below (the assumptions made are detailed in Appendix 10). A selective harvesting scenario is described. Unless otherwise acknowledged, all parameter values are based on empirical data (Chapters 2 to 5).

6.2.2.1 Initial woodland population and individual plant attributes

The density, species composition and relative abundances of the initial woodland population was based on empirical data collected in Manyeleti, the protected area immediately adjacent to Thorndale, representing savanna woodland protected from live wood harvesting. The model currently considers three generic woody plant species or plant functional types differing from one another in life-history characteristics, growth form and attractiveness to harvesters and browsing livestock (by changing certain assumptions the responses of other species types can easily be assessed):

1. tall, single-stemmed woody plants with relatively light density wood and bearing edible fruit;
2. medium-height, single-stemmed woody plants, favoured by harvesters for their dense wood;
3. short to medium-height, multi-stemmed 'bushy' woody plants, with a light density wood.

The occupants of each cell (and the duration of their occupancy) are determined by rules reflecting functional group specific attributes, including seed dispersal distances and number of seedlings produced per reproductively mature woody plant, attractiveness to harvesters or browsing livestock, resprouting vigour and estimated longevity. Attributes of each functional group were defined using a species considered to be representative: *Sclerocarya birrea* for the first, *Combretum apiculatum* for the second and *Combretum collinum* for the third.

Initial population structures (represented by stem diameter size frequency distributions) were randomly chosen from an exponential function around species-specific mean diameters:

$$D_i = -D_m \ln(1 - r),$$

where D_i is the stem diameter (cm) of the ‘new woody plant’ (composite stem diameter if the plant is multi-stemmed) in grid cell i ; D_m is the species-specific mean stem diameter (cm); and r is a random number drawn from a uniform distribution (where $0 \leq r < 1$). Stem diameters were converted to size classes (placed within size class bins with size class number and interval sensitive to species-specific longevities, and correlated to wood density and surmised growth rates) using a hyperbolic function (i.e. small individuals grow faster than larger ones in relative terms, with growth slowing as plants near the species-specific maximum diameter. Thus, under optimal environmental conditions, woody plant diameter (D) and time (t) are assumed to be hyperbolically dependent on one another (until the plant reaches the species-specific maximum diameter (D_x)), with a constant (k) reflecting growth within a year of favourable growing, primarily rainfall, conditions:

$$D(t) = t * D_x * (k/L + 1) / (k + t),$$

Following this relation, there are L (L being the relative species-specific longevity, estimated in years) different possible diameter values for each time step. Since the model works in annual time steps, these L diameter values were identified as the centres of L size classes (SC). Following this approach, the SC to which each woody plant’s diameter (D) belongs can be derived using:

$$SC = Dk / ((D_x(k/L + 1) - D)),$$

therefore as D tends to zero the woody plant will be represented by the smallest size class, while woody plants reach their maximum diameter at the species-specific maximum age.

The woody plants constituting the initial populations were given an age equivalent to the stem diameter size class into which they fell, with the assumption that they

had experienced good growing conditions and constant growth throughout their lifetimes. By assigning individual woody plants both an age and a size class it is possible to get an indication of the extent to which they subsequently have been suppressed by unfavourable growth conditions or damage, i.e. from browsing, harvesting or fire.

The height of 'new woody plants' was determined using regression equations of the allometric relationship between height and stem diameter (Chapter 3):

$$\text{Log}_{10}H = a + b \cdot \text{log}_{10}D,$$

where H is woody plant height (m); D is stem diameter (cm); a and b are species- (and size-) specific coefficients.

Woody plant biomass was calculated following the equation of Netshiluvhi & Scholes (2002) (based on the allometric equations of several authors for broad-leaved woody plant species):

$$B = 0.035 \cdot D^{2.5},$$

where B is woody plant biomass (kg) and D is woody plant diameter (cm).

Woody plants become reproductive once they exceed 'reproductive size', a definition based on observations by Shackleton (1997) that some individuals begin reproducing once they are one fifth of the species-specific maximum height, whilst at two thirds of a species' maximum height all individuals have attained reproductive maturity. As a compromise in the model, individuals begin reproducing once they reach a height exceeding 0.58 of the species-specific maximum height. A species-specific mean number of seeds (or rather seedlings, as described below) is produced by each reproductively mature woody plant. Currently the model does not account for the influencing of woody plant size on the number of recruits produced per reproductive individual.

6.2.2.2 Rainfall

The variable annual rainfall experienced in semi-arid savannas was simulated by first determining from the literature the mean annual rainfall (mm) considered to define a dry, average or wet rainfall season. These means were bracketed by equivalent ranges and a rainfall model, interpolating data from rain stations for southern Africa (McNeill *et al.* 1994), and were used to simulate annual rainfall over 100 years for the latitudinal/longitudinal location of the study area. The relative probability of experiencing a dry (0.34), average (0.47) or wet (0.19) season was then determined. Rainfall is applied evenly over the entire grid, this being a reasonable assumption given the size of the area modelled. Plant growth is rain limited, and rainfall from the previous season determines seed production and seedling establishment of the current season. For the first year of the simulation, previous season rainfall is set at average, ensuring some woody plant growth and reproduction during this first year.

6.2.2.3 Woody plant growth

During years of poor rainfall, woody plant growth is assumed to be insignificant. In years of average or wet rainfall, woody plants 'grow' by a size class (Figure 3 on page 180). As previously described, size class intervals are species-specific and correlated with longevity and wood density (and anticipated growth rates). The new size class by which an individual is represented is used to calculate stem diameter size (in effect a mean stem diameter for that size class), following which it's new height, biomass, and reproductive status are determined. Suppression of growth of smaller individuals (less than a meter in height) through browsing by livestock (goats and cattle) is considered to be important close to the settlement (less than 500 m). For these individuals growth only occurs during years of above-average rainfall when grass is expected to be abundant and preferred by livestock and browsing damage therefore minimal. At the end of the woody plant growth sub-module the total biomass of each species' population is calculated, together with the total biomass of all woody plants within the study area.

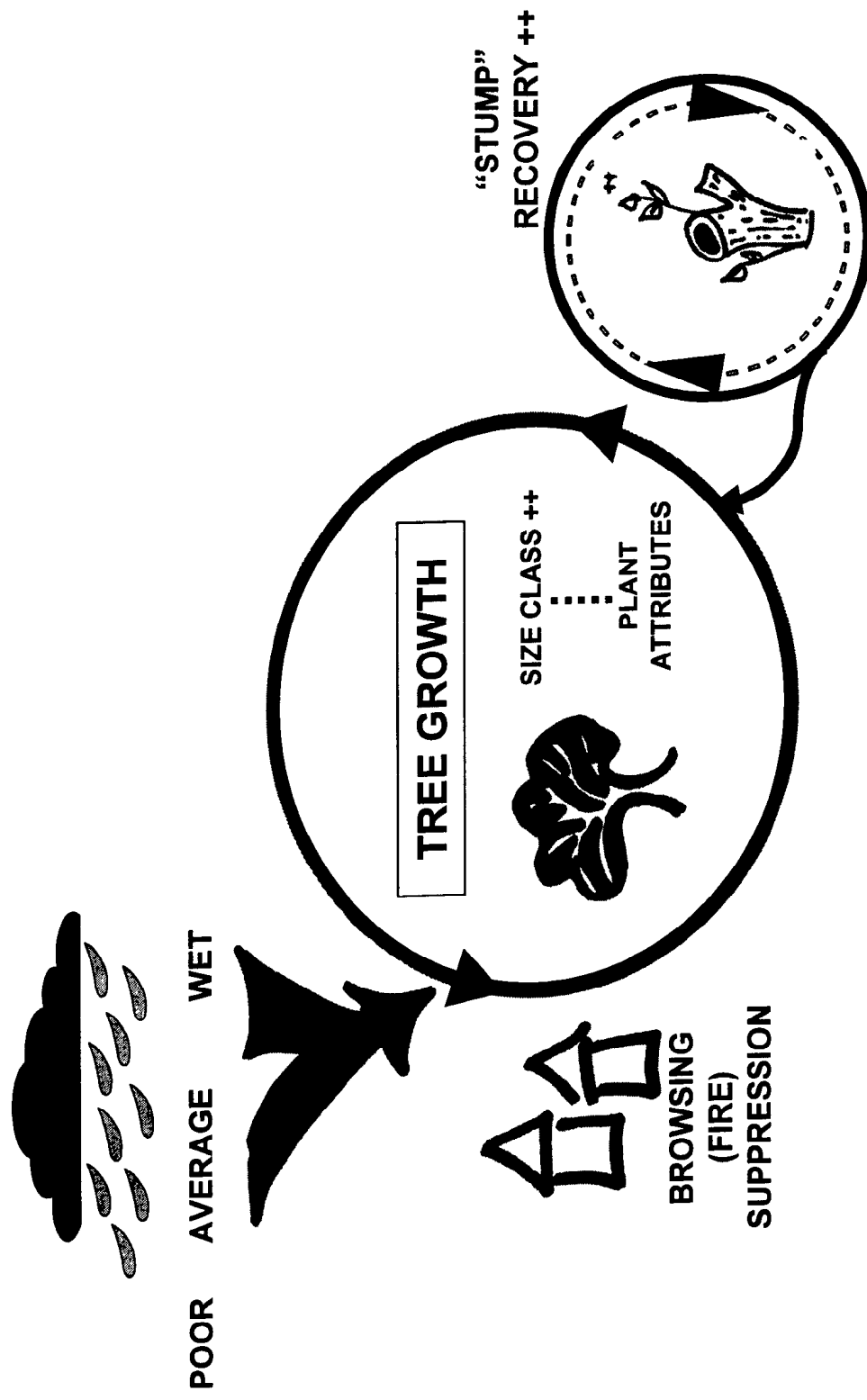


Figure 3. Diagram of the modelled variables influencing woody plant growth. With each increase in stem diameter class other plant attributes, i.e. reproductive status, are recalculated. Once a woody plant has been harvested, it takes several years to recover and resume 'normal' woody plant growth.

6.2.3 Wood biomass production and fuelwood demand

The initial woody plant population is unharvested. Additionally, it is assumed that there has been an accumulation of deadwood, and based on Shackleton's (1997) observations for semi-arid savanna woodlands, this deadwood can be estimated to be 303.5 kg ha^{-1} or 9105 kg for the area simulated by the model. The annual fuelwood requirement of Thorndale amounts to 296 019 kg. All fuelwood is obtained from the woodlands surrounding the settlement. As the simulated transect represents 2.5% of the woodland area, this translates into 7400.5 kg of fuelwood that must be harvested from the simulated area each year. Fuelwood demand is incremented according to population growth (estimated at 2.4% for the study region (Pollard *et al.* 1999)) and the number of additional households. The amount of wood currently extracted by non-residents is insignificant, although as has already happened in settlements less isolated than Thorndale, this is likely to change.

6.2.3.1 Woody plant harvesting

Each individual woody plant is assigned a 'utility' value (updated annually following woody plant growth) that represents its value to harvesters for fuelwood:

$$U = P(D/D_x)(1 - ((1 - q)/r_x)r)C + s,$$

where U, woody plant 'utility', is a relative value between 0 and 1, composed of a product of 'desirability' (P): how desirable a particular species is for fuelwood (dependent on species-specific properties such as wood density; growth form e.g. multi-stemmedness and harvester's preference); its size: D is the stem diameter of the individual; D_x , the species-specific maximum diameter; its distance from the settlement: q is a constant (value set at 0.1) allowing woody plants at the furthest extreme of the transect to be harvested, although infrequently; r_x is the furthest extreme of the transect from the settlement; whilst r is the position of the woody plant along the transect, relative to the settlement; C is woody plant 'cut history' (value $> 0 < 1$), representing the number of times the individual has previously been cut: woody plants that have been cut several times becoming more multi-

stemmed and of less value to harvesters. As harvesters cannot have perfect knowledge of their environment, nor infinite energy, a random number (s) with a Gaussian distribution is added to simulate harvester 'behaviour' (data with sampling errors and expected deviations from a mean (mean = 0.1; SD = 0.05)). For woody plants that have been cut and have not yet recovered their lost biomass, woody plant 'Utility' value is reduced relative to how recently they were cut and how much they have recovered:

$$U_s = U(R/R_t),$$

where U_s , the 'Utility' value of cut woody plants (referred to as 'stumps'), is the product of the 'Utility' value (U) of the woody plant prior to its being cut and a term reflecting the number of years of favourable growing conditions that have passed since cutting (R), relative to the total amount of recovery time (R_t , also in years) required for it to lose its 'stump status' (dependent on stem diameter size) and resume 'normal' woody plant attributes.

Woody plants are ordered according to their 'Utility' values. It is assumed that deadwood is collected before any live wood harvesting occurs (Figure 4 on page 183). If, after all deadwood has been used fuelwood requirements have not been met, selective live wood harvesting takes place: individuals with the highest 'Utility' values being harvested first. The amount of fuelwood needed is reduced by the biomass of each woody plant harvested until no more wood is needed for that year (or when there are no more woody plants left!). A woody plant's harvested biomass is calculated by:

$$B = B_t - w((\pi(D/2)^2 v)/104),$$

where B is biomass harvested (kg): a function of B_t , the woody plants total biomass prior to being cut minus the biomass remaining behind in the woody plant stump. If it is assumed that the woody plant stump can be represented by a cylinder, the mass of the woody plant stump can be calculated by multiplying its density (w - species-specific wood density, kg/m^3) by its volume: $\pi(i)$ multiplied by the stump radius (half the diameter (D)) squared and multiplied by the height at which the woody plant was cut (v , set here at 0.5 m)

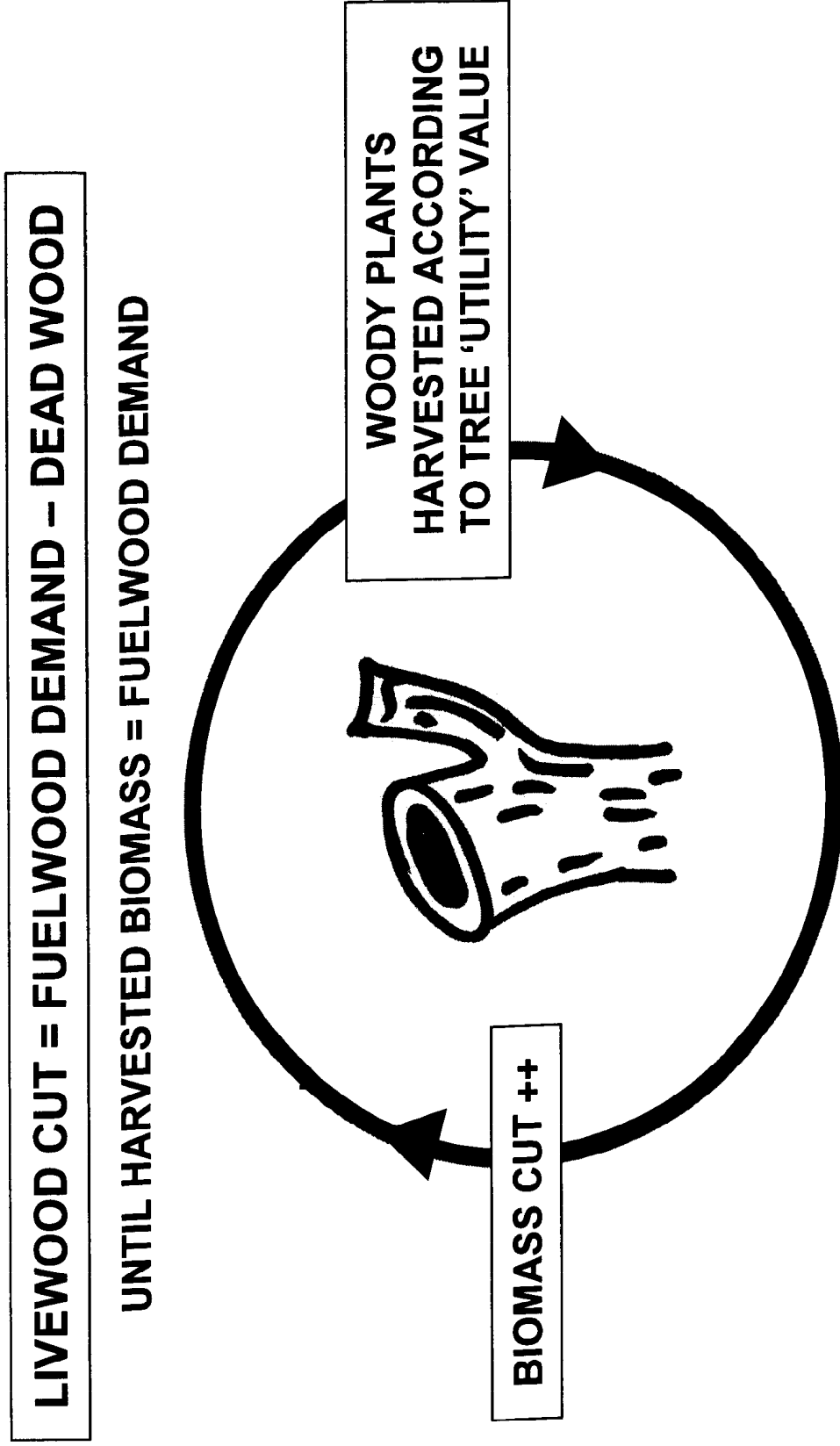


Figure 4. Diagram of the modelled live wood harvesting process. The attractiveness of woody plants to harvesters is given in their 'utility' value. The amount of live wood harvested is reduced by the quantity of deadwood produced during the previous year.

Once the woody plant has been cut its cut history is incremented by one; woody plant biomass and height are reduced to that of the remaining stump; and it is non-reproductive

6.2.3.2 *Stump recovery*

Once woody plants have been harvested they gain 'stump status' until they have 'recovered' (Figure 3 on page 180): recovery time being dependent on stem diameter size i.e. smaller woody plants (defined here as less than a third of the species-specific maximum stem diameter) need three years of favourable growing conditions (average or wet rainfall seasons); intermediate-sized woody plants (less than two thirds of the maximum stem diameter) need six years, and larger woody plants require nine years. During this period of time the woody plant's stem diameter does not increase, the assumption being that all resources are channelled into recovery of lost stem height. Cut woody plants close to the settlement (less than 500 m away) are additionally vulnerable to browsing livestock (as in the woody plant growth sub-module): only in years of above average rainfall do they escape browsing and reduce their recovery time. Once recovered, an individual's attributes i.e. height; biomass and reproductive status are recalculated.

6.2.3.3 *Woody plant ageing, mortality and deadwood production*

Woody plants die and contribute to deadwood: (i) if rainfall is poor and woody plants are less than one year in age i.e. seedlings not yet well-established and vulnerable to wet-season drought (Higgins *et al.* 2000); (ii) woody plants that senesce (i.e. reach their species-specific longevity and die of old age); (iii) during years when rainfall is not abundant, a certain amount of 'background mortality' occurs (set here at 3%, based on data from Shackleton (1997)) of individuals with a height less than two metres (larger individuals experience little mortality from fire; desiccation etc.) (Figure 5 on page 185). Currently, the model does not explicitly simulate changes in grass biomass in response to rainfall and the subsequent incidence and effect of fire. This could easily be incorporated (Higgins *et al.* 2000). The assumption was made that close to settlements, grass biomass is kept low by grazing livestock and therefore the effect of fire on woody plants will be limited. Further away from the village, grass biomass is higher and fire may

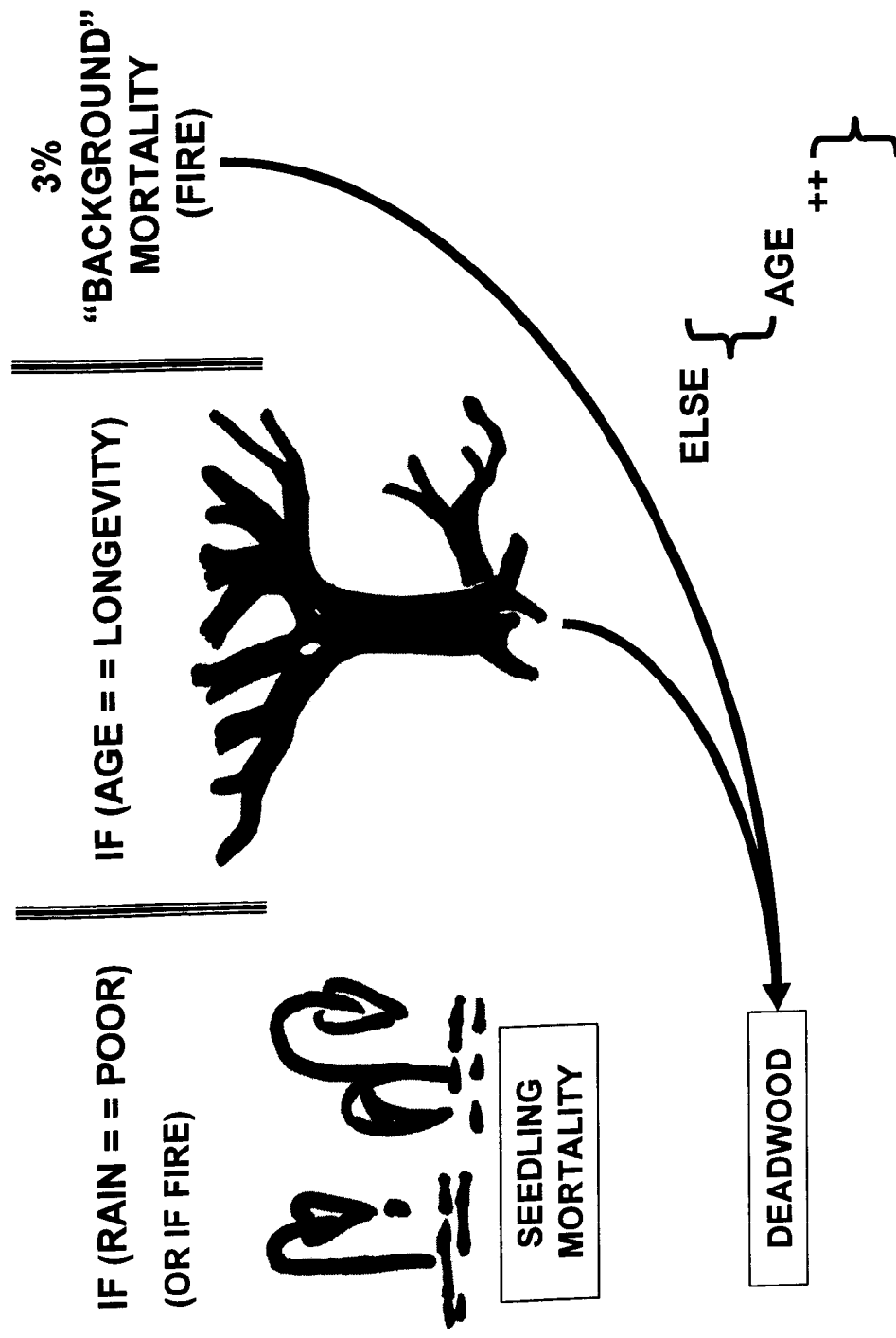


Figure 5. Diagram of the modelled process of woody plant mortality and ageing. Seedlings are vulnerable to dry periods or the incidence of fire. Larger woody plants experience a small amount of 'background mortality' from fire, repeated harvesting and browsing or extensive drought periods, or they senesce once they have completed their expected lifespan. Surviving woody plants age by a year with each time step.

result in the mortality of small woody plants. This mortality is included in the above-mentioned ‘background mortality’ which is greatest for woody plants less than two metres in height (especially seedlings), located at distances greater than 2 km from the settlement.

Surviving woody plants age by a year; contribute 1.7% of their biomass annually to the total deadwood produced (Shackleton 1997), and are represented by measures of species abundance, population structure (number of individuals per stem diameter size class) and the proportion of the population (by size class) composed of individuals with a ‘stump status’.

6.2.3.4 *Seedling dispersal*

The model does not consider the pre-seedling life stages of woody plants (i.e. number of seeds produced and their fate including the proportion actually germinating) and instead focuses on seedlings ‘dispersed’. As previously mentioned, seed and subsequent seedling production of a current year is dependent on the amount of rainfall received during the previous season: if rainfall of the previous season is not poor, woody plants that are reproductively mature produce seedlings (Figure 6 on page 187). The number of seedlings (S) produced by an individual woody plant can be written:

$$S = Rm \pm d,$$

where S is dependent on the amount of rainfall of the previous season (R, set here at 1 for years of average rainfall and 2 for years of abundant rainfall i.e. more seedlings are produced in years following above-average rainfall) and varies according to a species-specific mean number of seedlings (m) by a species-specific standard deviation (d).

Each seedling is dispersed a species-specific mean dispersal distance from the parent plant to surrounding cells (in a randomly selected direction as data from regional weather stations shows that there is no dominant prevailing wind direction) that are either empty or containing other seedlings. Seedlings are represented by the first size class; have an age of zero, and a species-specific stem

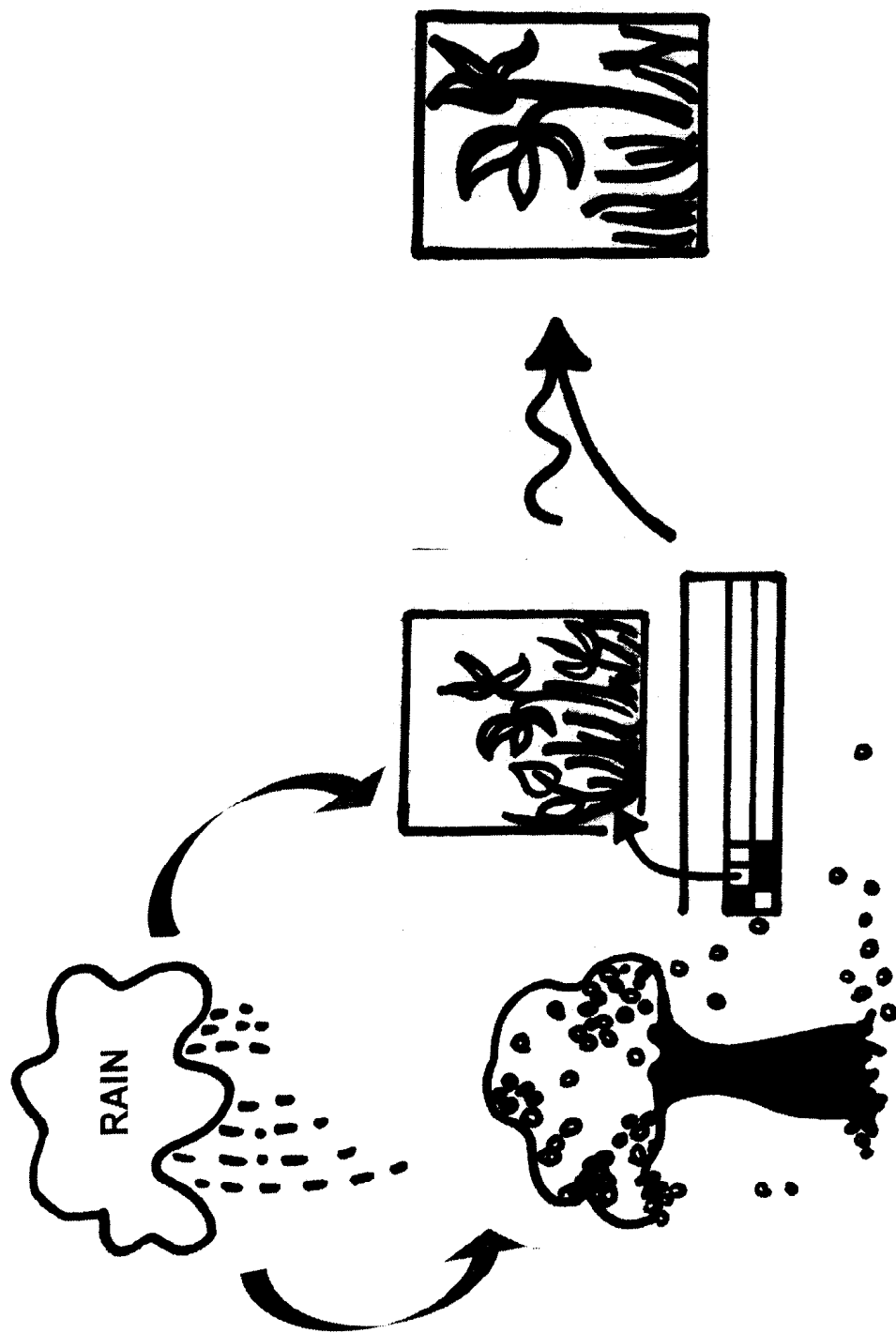


Figure 6. Diagram of the modelled process of seed dispersal and establishment. Seed production is determined by rainfall of the previous season. Seeds are dispersed to empty grid cells or grid cells containing other seedlings within the species-specific dispersal distance of the 'parent'. Competition between seedlings ensures that only a single seedling establishes in each grid cell. Competition with grass cover may additionally influence seedling establishment.

diameter and height. An addition to the model would be to model shade-tolerant seedlings surviving in cells containing larger woody plants, persisting beneath their canopies and attaining reproductive status only once the larger plant had died.

6.2.3.5 *Seedling establishment*

For cells that contain more than one seedling, simple lottery competition determines which seedling ‘wins’ and will become established: the probability of a particular species being represented by the ‘winner’ is determined by dividing the number of seedlings per species by the total number of seedlings in that cell. Once the ‘winner’ has been determined, all other seedlings die. The species represented by the most seedlings will have the highest probability of becoming established. The probability of seedlings establishing is dependent on the rainfall of the following season and negatively influenced by the incidence of fire and a high grass biomass. Grass biomass increases with distance from the settlement (Appendix 3) and is associated with a greater probability of fire.

6.3 GAPS IN UNDERSTANDING AND KNOWLEDGE OF SAVANNA WOODY PLANTS

Through developing the woodland model, the important information gaps identified were:

1. *growth rates*: crucial to understanding woody plant population dynamics, productivity and response to damage and therefore essential for sustainable management. Growth rates of different plant stages, e.g. seedlings versus larger woody plants, are likely to differ with different growth allocation ‘strategies’; species with denser wood are likely to grow more slowly. The rate of woody plant growth is important in determining the length of time during which it is exposed to browsing or fire damage.
2. *longevity*: most savanna woody plants cannot be aged using counts of annual rings. For long-lived organisms it is difficult to determine longevities. Wood density was considered to indicate the possible life span of a species, i.e. organisms with denser wood were likely to live for longer.

3. *time to recovery*: it would be valuable to know how long different woody plant species take to recover following harvesting, i.e. for their repeated harvesting.
4. *repeated harvesting*: the effect of repeated harvesting of a woody plant is not known. It is possible that at certain periods in the seasonal cycle, once belowground stored resources have been depleted through resprouting and recovery of lost biomass, further harvesting (or the effects of fire, herbivory and drought) may result in plant mortality.
5. *coppice/resprout shoot growth rate*: information on coppice growth rates of different savanna woody plants would be valuable for resource management. Chapter 5 documents coppice output over a relatively short time period following harvesting but longer-term data would be valuable, including experimental pruning of coppice shoots to determine the influence of apical dominance on coppice output.
6. *age of resprouting*: it is not known at what age it is possible for a woody plant seedling to resprout, and survive, following damage. The amount of belowground reserves that the seedling has managed to store is likely to be critical.

6.3.1 Expected model outcomes

Using graphical output, including (i) the relative abundance of different species/plant functional types; (ii) population structures (stem diameter and height size class distributions); and (iii) recruitment capacity (the number of reproductively mature individuals), the model will be used to examine changes in the woodland. These may include:

1. Changes in the abundance or dominance and patterns of distribution of certain woody plant species/functional types under alternative scenarios, including no harvesting. It is likely that favoured fuelwood species, which generally have a relatively dense wood, will take the longest to recover following harvesting. This might lead to a shift in species/functional type dominance, with those considered less attractive by harvesters (in this case represented by the light-wooded, multi-stemmed *Combretum collinum*)

dominating. Perhaps a diversion of harvesting attention from rare species will support their recovery.

2. Shifts in woodland vegetation height structure, e.g. from a range of heights (in the case of a multi-species/-functional type community) to a 'bushland' composed of short, multi-stemmed plants (dominated by a single species/functional type).
3. 'Bottlenecks' in seedling establishment and recruitment into the reproductively mature population, as a result of harvesting, browsing or other damage, influencing the persistence of species/functional types.
4. In response to alternative harvesting strategies, with the objective of determining which are most likely to be successful in ensuring the continued availability of favoured fuelwood species.

6.4 CONCLUDING COMMENT

As pressures on savanna woodland resources intensify, an understanding of the factors influencing woody plant regeneration and species persistence is critical for the effective management of favoured fuelwood species. The described model is versatile, parametised from empirical sources, and easily adapted to other woodland contexts using the appropriate information. The woodland model is considered to have potential as a valuable management tool, enabling a deepening of the understanding of woodland systems, highlighting the gaps in that understanding, and offering a predictive approach to the assessment of alternative resource management strategies.

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CHAPTER 7

Synthesis and General Discussion

THE REGENERATION ECOLOGY OF SAVANNA WOODY PLANTS IN RELATION TO HUMAN UTILISATION

This concluding chapter sets out to:

- Integrate the ecological findings of the study's components and their synthesis in the model formulation exercise and the additional insights gained through discussions with resident resource users (using Participatory Rural Appraisal (PRA) techniques).
- Discuss the contribution made by the study to the understanding of savanna woody plant regeneration ecology.
- Identify the potential management implications of the study's findings in light of the continuing importance of woody plant resources for the livelihoods of rural people.

7.1 INTRODUCTION

“Disturbances are major sources of both temporal and spatial heterogeneity in the structure and dynamics of naturally occurring systems” (Sousa 1984)

7.1.1 Recovery following disturbance: ‘natural’ versus human-related disturbances

Disturbances have profound effects on the dynamics of plant populations by influencing recruitment, mortality, dominance and distribution (Harper 1977). In African savanna woodlands, disturbances include grazing, browsing and trampling by wildlife and livestock, anthropogenic clearance of woodland vegetation for cultivation, the harvesting of trees for different purposes and the initiation of fire (Frost 1996). An investigation of the regenerative ability of savanna woody plants in relationship to their utilisation by humans would be incomplete without an assessment of how these human-related disturbances (or pressures) differ in nature from previously dominant ‘natural’ disturbances, and the plant traits that enable woody plant species to endure such pressures.

Previous to intensive human-related disturbances, fire would have been one of the most important agents influencing woody plant population dynamics (Trollope 1984). Additionally, large ungulates (particularly elephants) may have damaged the plants on which they browsed (Owen-Smith 1988). In general, smaller plants have a higher probability of being killed by both fire and herbivores, with the impact of either likely to differ seasonally, e.g. the incidence of fire will be higher following a good rainfall season and hence greater herbaceous biomass (fuel load) accumulation. The large underground biomass of savanna woody plants (with 50 to 80% of plant biomass belowground) allows plants to survive and recover following the loss of aboveground biomass (Rutherford 1983). Other plant traits associated with limiting and surviving damage may include: a denser wood; the ability to resprout; the ability to more rapidly recover lost aboveground biomass; and the ability to reproduce vegetatively (Walker & Noy-Meir 1982, Walker 1985).

Humans alter the frequency, intensity and extent of fires (Scholes 1997). Humans ignite fires, accidentally or intentionally, so that they occur more frequently than through 'natural' forms of ignition (e.g. lightning strikes). Their livestock consume grass, reducing fuel load and therefore the intensity and extent of subsequent fires and their impact on woody plants. In the woodlands surrounding the settlements of the study region, live wood harvesting has clearly surpassed fire in importance as a determinant of woody plant population dynamics. As humans are relatively sedentary, the effects of their resource utilisation are concentrated. They gather deadwood and selectively cut woody plants, removing a higher proportion of live wood biomass than would be lost to fire in most cases. Growing human populations, continuing to depend on fuelwood as their primary energy source, exert increasing pressures on woody plant populations. Harvesting occurs throughout the year although it is likely to be greater during the winter when additional fuel is needed to counter the cold (Dovie *et al.* 2004). At this time, stored belowground reserves may be relatively low after a potentially lengthy dry period, possibly influencing plant survival and biomass recovery. Harvested woody plants are additionally more vulnerable to browsing with resprout shoots frequently accessible to livestock. Independently and in combination, harvesting

of woody plants and browsing by livestock may prevent woody plants from growing beyond a vegetative state, with implications for long-term population recruitment.

The characteristics of woody plants that enable them to endure fire or herbivore damage conceivably also equip them to survive the loss of aboveground biomass from live wood harvesting. However, when the levels of human use exceed the regenerative ability of woody plants, the diversity and productivity of the system may be reduced. The effects of human disturbances are likely to differ for species depending on how heavily they are affected, the duration of the impact and their ability to recover following damage. Certain species may be favoured, more accessible or sensitive to disturbance than others and may become locally extinct with increasing human disturbance.

7.2 INTEGRATION OF ECOLOGICAL FINDINGS AND ADDITIONAL INSIGHTS

7.2.1 Savanna woody plant population structure in relation to human utilisation

Wood harvesting in the communal rangelands of the study region has reduced woody plant densities and live wood biomass and altered woody plant growth form. Plants of many species were more highly branched than in protected areas, of a shorter stature and more likely to be non-reproductive. Other studies have suggested that such changes in vegetation structure and wood biomass indicate a potential loss of species and ecological function (Lykke 1998, Shackleton *et al.* 1994). The population structures of the study species most heavily harvested have been altered through the selective removal of intermediate size ('pole' and 'small reproductive') stems. It follows that future regenerative potential may be limited by an absence of recruitment into the reproductively mature component of the population. Species that were previously protected from harvesting are now being cut as other sources become scarcer (e.g. the marula *Sclerocarya birrea*). All the study species were present across the study region with no species loss as a

consequence of harvesting documented, however, there was evidence of a shift in species dominance. *Terminalia sericea* had been heavily harvested in the communal rangelands surrounding settlements, probably due more to its accessibility (growing in monospecific stands) than to its value as a fuelwood. As a consequence, woody plant densities were lower than in adjacent protected areas, and plants were smaller and more highly branched. Those species highlighted by residents as providing valuable fuel and construction wood, were also perceived to have declined as a result of harvesting pressure (Appendix 11). These included the leadwood *Combretum imberbe* and the wild teak *Pterocarpus angolensis*, neither of which were amongst the study species due to their paucity. Of the study species, *Albizia harveyi* may be the most vulnerable to human utilisation pressures due to its seemingly poor regenerative capacity. Few seedlings were found in communal rangelands and in contrast to other species, resprouting response was relatively weak following cutting.

These patterns of vegetation change were clearly associated with a gradient of resource utilisation, decreasing in intensity with distance from settlements. Such observations are not unique to this study, with other studies previously carried out within the study region and elsewhere in southern and eastern Africa, having documented similar vegetation changes (Liengme 1983, Skarpe 1990, Shackleton *et al.* 1994, Higgins *et al.* 1999, White 1999, Luoga *et al.* 2002, Obiri *et al.* 2001). They are also in agreement with observations voiced by resource users of woodland change and diminishing wood resources (Appendix 11). The study contributes baseline information for several woody plant species, valuable for assessing current status and for subsequent monitoring and predicting of change.

7.2.2 Woody plant regeneration

Despite the evident impact of human utilisation on the density and population structure of those species most frequently harvested, the study species appear to have a high regenerative potential and could be considered capable of incorporating this damage within their natural functioning at present utilisation levels. There was some evidence suggesting that there may be compensatory regeneration following intensive woody plant harvesting, although this was

inconclusive. Fundamentally, population dynamics appear to continue to be driven by underlying environmental variables (particularly rainfall) rather than the anthropogenic factors associated with communal rangelands. If resource utilisation is effectively managed it is likely that long-term harvesting will have no permanent impact. However, the possibility of a reduction in pressures on woody plant resources seems unlikely for the foreseeable future (Lawes *et al.* 2004). Although communal settlements are rapidly becoming peri-urban, the inhabitants exert and will continue to exert pressure on the natural resources of the study area.

7.2.2.1 Seedling establishment

The study provides evidence to support the theory that herbaceous cover limits both woody plant seedling emergence and survival. Grass competes directly with seedlings for limited soil moisture and influences seedling exposure to herbivores. Following an exceptionally good rainfall season, cohorts of seedlings of most of the study species established. In general, the study species appear to require similar conditions for seedling establishment, with soil water availability plausibly the most important determinant. Some species may be more successful at colonising disturbed areas, e.g. a higher proportion of *T. sericea* seedlings established in the open than seedlings of other species; *Strychnos madagascariensis* seedlings appeared to be relatively more tolerant of limited water availability (during the factorial experiment). In addition to desiccation, young seedlings are highly vulnerable to damage by fire and herbivores. Residents participating in discussions about the wood resource base unanimously agreed that fire is an important factor resulting in mortality of the small seedlings of all species. Seedlings were held to be more capable of enduring livestock browsing damage, although *Sclerocarya birrea* seedlings were considered vulnerable. Small *S. birrea* seedlings were more abundant in protected areas despite the relative abundance of large reproductively mature plants in communal lands. Through the food and protection (in the case of rodents) it offers herbivores and the fuel it provides for fires, grass biomass influences the exposure of woody plant seedlings to damage and hence the resultant seedling densities and spatial arrangement.

For all species, analysis of population size structures provided little evidence that episodic recruitment was a major influential or differentiating factor. The differences between woody plant population structures in communal and protected area sites were not substantial. Possibly, the size frequency distribution analyses were not sufficiently sensitive. It is also plausible that influential factors operate across land use (especially rainfall) or that different factors associated with either land use have similar outcomes for woody plant growth, recruitment suppression and resultant population structure.

7.2.2.2 *Resprouting ability*

All the study species resprouted following harvesting and there was no harvest-induced mortality. Generally, the resprouting response of species was channelled into either many, small or relatively fewer, larger resprout shoots, with the composite resprout shoot diameter being approximately similar across species, although amongst the study species there were clearly some that were more vigorous resprouters than others. Resprouting output increased with plant size (confirmed in the PRA discussions). The height at which plants were cut influenced the origin of resprouting shoots but not their number. PRA information suggested that cutting at a greater height improved resprouting output and plant survival. The ability to resprout and persist is important in a context of frequent disturbance, especially when conditions for seedling establishment are dependent on erratically favourable rainfall conditions.

7.2.3 Woody plant response groups

Although the number of species examined by this study is undoubtedly insufficient to decisively group species according to differences in their regenerative abilities, growth strategies and response to damage, some broad generalisations emerged which are worth articulating and possibly researching further.

- The species with relatively higher numbers of seedlings are generally those species that attain a greater maximum height, are more likely to be single-

stemmed and appear to change their growth allocation at a certain height (from a focus on height gain to one of stem diameter increment). This shift appears to be coincident with the height at which woody plants are considered less vulnerable to fire and herbivores (PRA results support this).

Those species exhibiting a more vigorous resprouting response had fewer seedlings, were shorter and more multi-stemmed, and grew relatively more in composite stem diameter in relationship to height. It is possible that these species accumulate relatively larger belowground reserves, than the single-stemmed species described above, to survive disturbance within the flame/browse zone.

Dense wooded species were more favoured for fuelwood than those with a light wood. Interestingly, during the PRA sessions a distinction was made between 'dry' and 'wet' species. Dry species were found to be those with a higher wood density and a lower resprouting vigour than wet species. Conceivably, the selective harvesting of species with a denser wood could result in the dominance of light-wooded, frequently multi-stemmed species of less value as a fuelwood resource.

7.3 MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS

The high regenerative ability of the study species suggests that they can be effectively managed as a valuable fuelwood resource. Controlled harvesting of favoured fuelwood species would be required to prevent undesirable changes in community composition, recruitment conditions and the loss of reproductive plants. Future management would additionally need to take into consideration the differential effects of wood biomass loss on species for woodland diversity and resource availability to be maintained.

Management of the wood resource base might include the following approaches:

As several species are used for fuelwood, a rotational harvesting strategy may be effective. Woody plants in designated areas are harvested, while protecting sufficient reproductively mature plants and those of intermediate size to

facilitate future recruitment capacity – referred to elsewhere as “coppice with standards” (Grundy 1995). Harvested plants in other areas are protected from further harvesting or browsing until they have recovered their aboveground biomass or have produced resprout shoots of value for fuelwood.

- The short-term needs of rural communities are likely to preclude the long fallow periods required between harvests. Short-rotation forestry programmes for fuelwood production are required: planting small woodlots of fast-growing, non-invasive species may offer an effective additional supply of wood that would lift some of the pressure off indigenous woodlands.
- Protection of seedlings and small plants from livestock and fire would encourage population recruitment and productivity. Planting out of nursery-grown seedlings in suitable microhabitats could be undertaken, although this is likely to be labour and resource intensive.
- Enabling rural inhabitants to harvest the surplus wood biomass of nearby protected areas using sustainable harvesting techniques could be considered in some areas.
- The provisioning of alternative sources of energy (e.g. electricity - potentially available, but presently too expensive for the vast majority of impoverished village households) would reduce the pressure on woodlands. Previous attempts to introduce alternative cooking means to households in the region have not been successful (Shackleton & Shackleton 2000). Should alternative sources of energy be accepted and effectively distributed, they have the potential of simultaneously addressing the health risks associated with the inhalation of wood smoke, the wood biomass supply scarcity and land degradation.

Resprout growth following harvesting has the potential to contribute a considerable fuelwood resource. The study's findings suggest that the following methods would improve resprouting output and biomass productivity:

- Plants should be cut at a greater height. Resultant resprout shoots will originate from higher up and subsequent browsing damage may be limited.

- Selective harvesting of those plants having a greater resprout output (by species and size) should be combined with subsequent resprout management, so as to maintain the regenerative potential of woody plant populations.
- Pruning resprout shoots, preferably prior to dieback (within the first few months following harvesting), is likely to accelerate the growth of remaining shoots and reduce the harvesting interval (Shackleton 2001).

7.4 WOODLAND MODEL SYNTHESIS AND THE GAPS IN UNDERSTANDING

The formulation of a model that can be used to simulate woody plant population dynamics in response to human utilisation was valuable in combining the study's ecological findings, while highlighting the gaps in our understanding. The conceived structure of the model is highly flexible, allowing it to be adapted for use in the study region or elsewhere, to examine different species or several syntopic species, and the consequences of alternative scenarios or resource management strategies.

The gaps in understanding, emphasised as being valuable for future research include:

- The effect of repeated harvesting on subsequent resprouting response and survival.
- The importance of the seasonal timing of harvesting. Plants may be more vulnerable to harvesting during certain seasons, or following extensive dry periods, when they have insufficient stored resources.
- The length of time required for a woody plant to recover lost biomass and attain reproductive maturity.
- Growth rates of woody plants of different species and size, an important variable in determining population dynamics and wood productivity. Growth rates additionally influence plant vulnerability to fire and browsers.
- The triggers for a plant to switch from storing belowground resources in roots to allocating growth to shoots.

- Woody plant longevity.
- The time interval between episodic recruitment events.
- The relative importance of vegetative reproduction for different woody plant species.

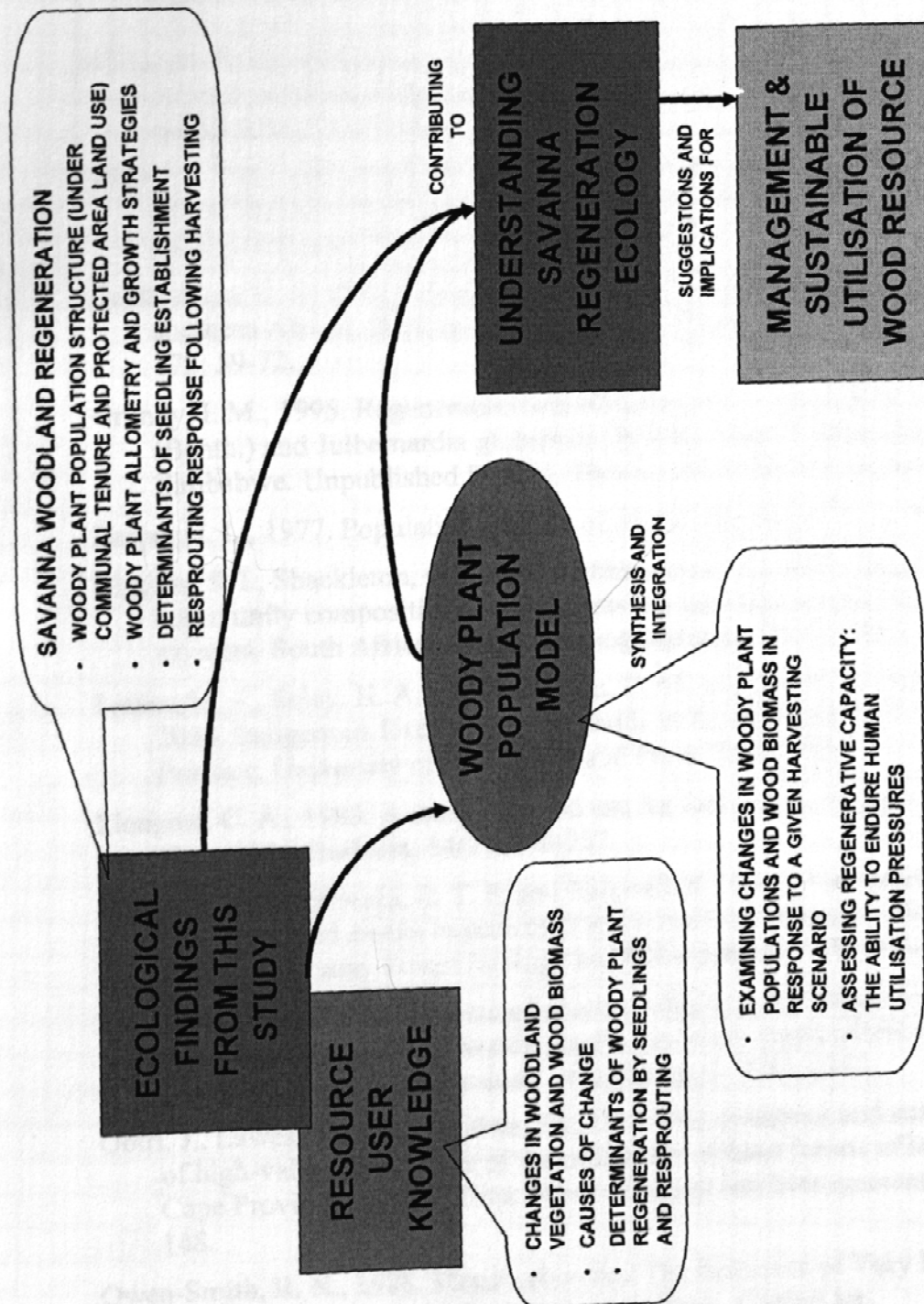
The diagram on page 205 may assist in contextualising the elements brought together in this synthesis.

7.5 SUSTAINABLE SAVANNA WOODLAND MANAGEMENT

The conclusions arising from this study provide several indicators for effective woodland management and sustainability. It is important to view communal rangelands as multi-purpose agricultural landscapes or ecosystems, with livelihoods dependent not on a single resource but on a suite of resources of fluctuating value and availability (Obiri *et al.* 2001). Agroforestry programmes that combine the controlled use of savanna woody plants with agriculture and livestock, together with small-scale woodlot planting, have a higher probability of enabling the sustainability of local sources of fuelwood, while maintaining ecosystem integrity. Assessing the ability of savanna woody plants to regenerate following their harvesting is especially pertinent in South Africa at a time when there has been a shift in the approach to the management of indigenous woodlands. The current increased emphasis on the sustainable extractive use of natural resources, particularly by local rural communities emerges from the growing recognition of the value of woodland resources for people's livelihoods and local economies, accompanied by a restructuring of the national institutions governing forests and woodlands and the development of a number of new policies and strategies for integrated management (Cousins 1999, Lawes *et al.* 2004).

Previously, the support for effective means of woodland management, and the application of fire and grazing by livestock, was largely lacking within much of the woodland biome (Geldenhuys 1997). The effect of colonialism followed by centralised, frequently authoritarian governments which did not recognise

traditional land tenurial systems, led to widespread open-access natural resource use and land degradation in Africa (Seymour 1984). Alleviation of poverty is the most obvious and essential step towards developing options for long-term resource sustainability, productivity and conservation. Indigenous land use practices are only viable if local communities depend substantially on natural resources, if they have security of land tenure and control over their local resource base, and if they retain a sufficiently high level of internal cohesion with community membership defined in relationship to land and resources (Luoga *et al.* 2002, Obiri *et al.* 2001, Lawes *et al.* 2004). Currently in South Africa, local institutional capacities are weak and need to be strengthened and supported by effective resource management strategies, to be effective in leading resource management (Shackleton *et al.* 2001). To be sustainable, woody plant resource management must be ecologically sound, economically viable and socially desirable. It cannot be achieved in isolation of an understanding of the influence of prevailing local, regional and global economic driving forces.



Contextualisation of the elements brought together in this synthesis.

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APPENDICES

APPENDIX 1. Patterns in Woody Plant Populations in relation to Human Use in a South African Savanna

Paper presented by Kirsten S. Neke at the Natural Forests and Savanna Woodlands Symposium III, 2002. Kruger National Park, South Africa .
(Cited as: Neke, K.S., 2002 in Chapter 2, REFERENCES)

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Abstract: An understanding of the effects of resource utilisation (primarily fuelwood harvesting and livestock browsing) on woody plant population dynamics, and more specifically their regeneration ecology, is essential to understanding woodland stability and resilience with direct implications both for species persistence and for people's livelihoods. Woody plant populations dominating the catenal uplands of communal lands in the Bushbuckridge lowveld were contrasted with those of adjacent protected areas. Generally, the woody stratum was dominated by members of the Combretaceae, such as *Combretum zeyheri*, *C. apiculatum*, *C. collinum* and *Terminalia sericea*, with other dominant species including *Dichrostachys cinerea*, *Sclerocarya birrea* and *Strychnos madagascariensis*. Land use alone could not explain differences in population densities and structure due to the high level of variation between sites within each land use. Consequently, both tree and stem densities were found not to differ significantly with land use for the 15 species examined. Size frequency distributions based on stem diameters, indicated similar population trends for most species, with "inverse J-shaped" curves in protected areas, whilst in communal lands the smallest diameter size classes were relatively poorly represented resulting in "humped" or "flattened" size class distribution curves. A third of the species investigated did not appear to be influenced by land use, having similar size class distributions for both land uses. In contrast, land use had a marked influence on individual plant morphology with most species having a significantly reduced diameter and height and more stems per tree unit within communal lands in comparison to individuals within protected areas. *T. sericea*, although having a higher tree density in protected areas had a higher stem density within communal lands, with significantly more stems per plant unit. The implications of these results for the regeneration and functional classification of the species examined will be discussed, both in relation to their vigour to persist damage through resprouting and their reproductive recruitment potential.

1. INTRODUCTION & CONTEXT

Within rural areas of South Africa, and particularly in former homeland areas, poverty and the environment are highly intertwined. In South Africa, more than 70% of rural households reside within the savanna biome (Shackleton 2001). In the Bushbuckridge district, falling within the Limpopo lowveld savanna and a part of the former homelands of Gazankulu and Lebowa, approximately 60-70% of the potentially economically active population are unemployed (Shackleton 2000). Natural resources contribute greatly to local livelihoods: providing energy and food security, supplementing incomes and saving cash (Shackleton 1999). Trees especially are relied on for multiple uses, with wood remaining the primary source of fuel for the majority of rural households (Shackleton 1993). High population densities, unemployment and extreme poverty are placing enormous pressures on savanna woodlands.

HUMANS IN ECOSYSTEMS

In ecological theory, a keystone species is a species that controls the environment and determines which other species can survive in its presence: casual observance would place humans into this domineering role and yet the current paradigm in ecology considers humans not as a keystone species, but as an external disturbance to a "natural system" (Farina 2000).

The concept of the Cultural Landscape arose relatively recently in landscape ecology, recognising the existence of landscapes in which:

"the relationships between human activity and the environment have created ecological, socio-economic, and cultural patterns and feedback mechanisms that govern the presence, distribution and abundance of species assemblages" (Farina 2000)

A significant fraction of biodiversity survives within these human influenced landscapes and yet, there is little understanding of their structure and functioning although (i) they are of ecological interest: communal lands, characterised by the intensive use of a variety of resources, especially for firewood and grazing, offer the ideal opportunity to investigate the response of savannas to prolonged and intensive disturbance (Shackleton *et al.* 1994), and (ii) this information is vital for sustaining ecosystem integrity, people's livelihoods and for the future of protected areas.

By way of illustration, the Kruger National Park is not an island isolated from its surroundings, and its long-term future will be influenced by what happens outside it: a degraded surrounding landscape will influence ecosystems within the park and intensify the pressures placed on the park for resources. Ultimately, it is likely that the future of the Kruger and other protected areas will be shaped by local people's perceptions of their value within their lives. The recently conceived Kruger to Canyon Biosphere Reserve may provide an integral platform, supporting a

landscape-level vision of ecosystem management and sustainable resource utilisation through the collaboration of resource users, including rural communities, private game farms and state-run conservation areas. The very obvious need is for large-scale poverty alleviation to relieve the dependency on natural resources, but in the interim an understanding of woodland regeneration ecology is imperative for management and conservation.

The focus of this research is to investigate the regenerative ability of savanna woodlands in response to human utilisation pressures (mostly fuelwood harvesting, but also browsing by goats and cattle), with a view to providing scientific backing for methods of resource and ecosystem management.

2. STUDY AREA

The research was conducted in the Bushbuckridge district in the southernmost part of the Limpopo Province, formerly the Northern Province and prior to that a part of the former homelands of Gazankulu and Lebowa.

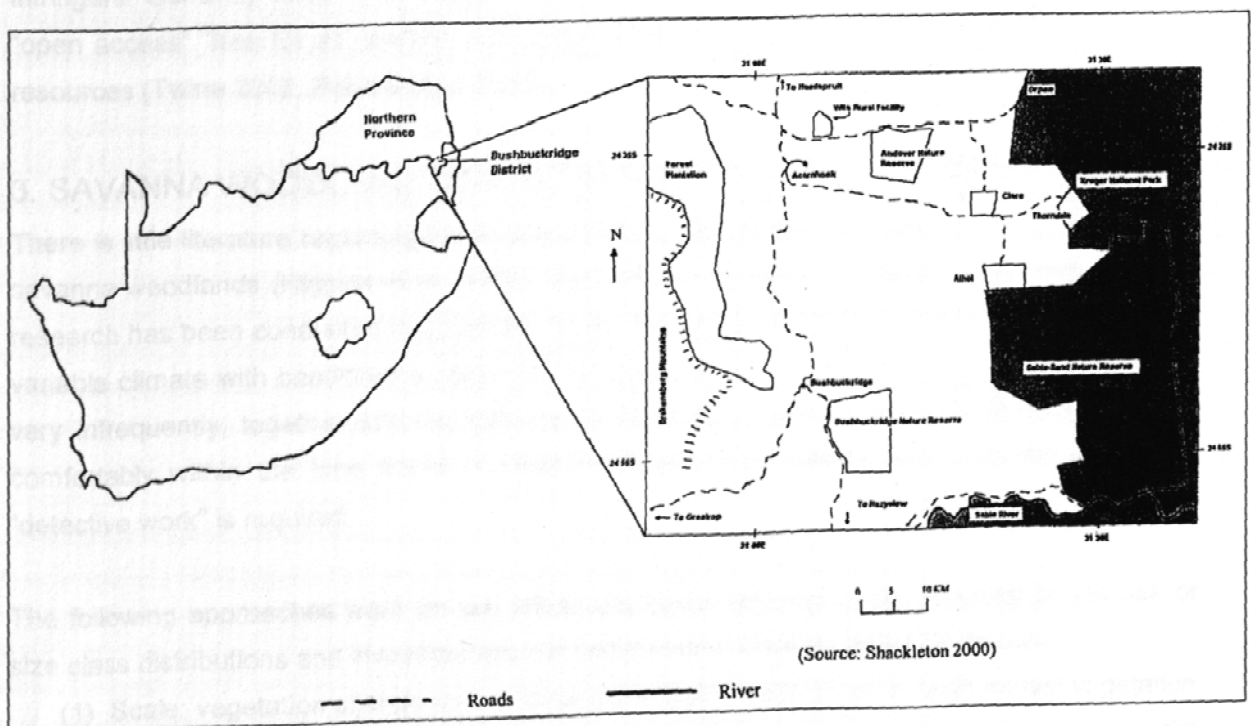


Figure 1. Map of Study Area falling within the Bushbuckridge District, delineated by the Drakensberg mountains in the west, the Kruger National Park in the east, the R531 road to the Kruger's Orpen gate in the North and the Sabi River in the South.

HISTORY (from Pollard *et al.* 1999)

During pre-colonial times the Lowveld was sparsely populated due to the prevalence of tsetse fly and malaria. In the 1850's the area was populated by sotho-speaking people, followed by tsonga-

speaking immigrants and then refugees as a consequence of war in Portuguese East Africa. In the 1930-1960's under the "Betterment & Villagisation" policy, "African Reserves" were created to control land. Blacks were removed from white-owned land and relocated to trust lands and grouped into centralised villages for better access to water, schools and clinics. Presently in Bushbuckridge, population densities and growth rates are high, and swelled by refugees from Mocambique. Unemployment is as high as 60-70%, there being limited local formal opportunities with a subsequent dependency on migrant labour.

ECOLOGICAL & SOCIO-ECONOMIC CONSEQUENCES:

Settlements are crowded, and there are severe water limitations with obvious implications for health and livelihoods. Degradation of ground cover and soil erosion reduce land available for cultivation and place constraints on cattle farming. There is an accelerating depletion of natural resources with the demand for fuelwood outstripping the supply of natural dry wood and resulting in live wood harvesting (Twine 2002). Prior to 1994 there was some control over woodland resources, with the Tribal Authority chief and "tribal police" controlling resource use and fining infringers. Currently there is an institutional vacuum with all control having degenerated into an "open access" "free for all" system, with external users adding to the rapid depletion of natural resources (Twine 2002, Pollard *et al.* 1999).

3. SAVANNA WOODLAND REGENERATION ECOLOGY AND RESILIENCE

There is little literature regarding the regeneration requirements and capacity of southern African savanna woodlands (Higgins *et al.* 2000), and less still for human inhabited woodlands as most research has been conducted in protected areas. The episodic nature of tree recruitment under a variable climate with conditions suitable for the regeneration of certain woody species occurring very infrequently, together with the difficulty of detecting seedlings in the landscape do not fit comfortably within the time frame of most (including PhD) studies and a certain amount of "detective work" is required.

The following approaches were (or are still to be) taken, with this paper focusing on the use of size class distributions and investigations into regeneration capacity (point (2) below):

- (1) Scale: vegetation change over a longer time period (assessed through annual vegetation surveys and local people's perceptions of vegetation change) and across a larger spatial area supplementing the more detailed population studies (Clarke *et al.* 1999).
- (2) Size Class Distributions: represent highly condensed indices of population dynamics acting over many years (Wiegand *et al.* 2000), allowing inferences (with limitations) to be drawn about species' response to disturbance and potential composition changes.
- (3) Functional Classification into Regeneration Syndromes based on life history traits. The ability of trees to regenerate following damage, either vegetatively or reproductively ~ "persistence vs recruitment" (Bond *et al.* 2001, Bellingham & Sparrow 2000).

- (4) Experimental work “accelerating” and enabling exploration of regeneration dynamics (exclosure experiment investigating factors influencing seedling recruitment; seedling transplantings investigating survival in communal lands under different intensities of livestock browsing and microhabitat conditions).
- (5) Ecological Modelling: an improved understanding of woodland dynamics on larger time scales and under different utilisation/management scenarios can be reached through the development of a spatially-explicit ecological model.

4. METHODS

Spatial variability in population density and structure was sampled in communal lands (heavily utilised by humans and their livestock) and adjacent protected areas. Sampling focused on Combretaceae-dominated granitic uplands falling within the area stretching from the western border of the Kruger National Park and Manyeleti Reserve west to the Wits Rural Facility and surrounds (Figure 1).

At each site (seven sites in communal areas and five in protected areas) sampling was in the form of eight 100 m long transects, of variable-width: 4 m wide for plants less than 4.5 m in height and 40 m wide for plants more than 4.5 m in height. Transects were positioned along a N-S compass bearing as randomly as possible.

For the fifteen dominant and economically important woody plant species selected (Appendix) the following variables were recorded: plant height; tree basal diameter (all stems of multi-stemmed plants were measured and used to calculate a composite tree stem diameter); the proportion of the plant harvested; evidence of browsing or fire damage; whether damaged plants had coppiced and position of coppice.

Population Size Frequency Distribution Analyses

Size class profiles were constructed following the methods of Condit *et al.* (1998) and Lykke (1998) with size classes defined to accommodate more individuals with increasing size, balancing the samples across size classes as the number of individuals declines with increasing size. The number of individuals in each size class is divided by the width of the class, giving the average number of individuals per size class category.

Statistical Analyses

Basic exploratory statistics (ANOVAs and Paired t-tests) were used to compare adjacent sites (for the 5 paired adjacent protected and communal sites), followed by more sophisticated analyses using the GLIMMIX macro in SAS® to perform Generalised Linear Mixed Modelling. For Count Data (multinomial/binary) i.e. tree densities and the proportion of trees falling within size classes, a model using Poisson error terms and a log link was fitted for data with a non-normal distribution.

Where there was overdispersion of the error data, a negative binomial model was used, the K factor (the aggregation parameter) being estimated using the method of Moments. The two models were compared using Aike's (AIC) information criterion and the best fitting model was used to make final inferences about the interaction between densities/size class profiles and land use. For Continuous Data i.e. heights and diameters, data normality was checked (Kolmogorov Goodness of Fit test) and where necessary (log) transformed, and variation in height and diameter due to land use was examined. Random variation was modelled using covariance structures and the best fit was determined using the AIC information criterion.

5. RESULTS

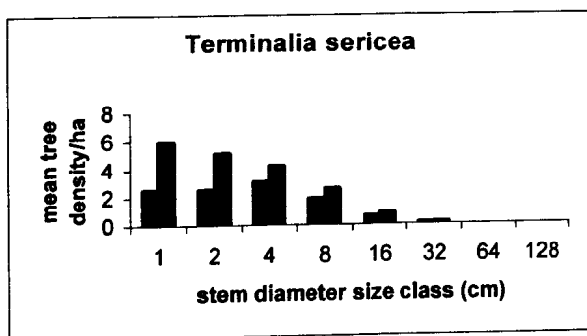
Density

Tree and stem densities for all selected species were found not to differ significantly with land use (Tables 1 & 2). Yet, most species have lower tree & stem densities in communal rangelands than in protected areas, particularly the most common species: *Dichrostachys cinerea*, *Strychnos madagascariensis* and *Combretum zeyheri*. In contrast *Combretum apiculatum*, *Combretum collinum* and *Peltophorum africanum* have higher tree and stem densities in communal than in adjacent protected areas. *Terminalia sericea* is interesting in that it has higher a tree density in protected areas but a greater stem density in communal areas.

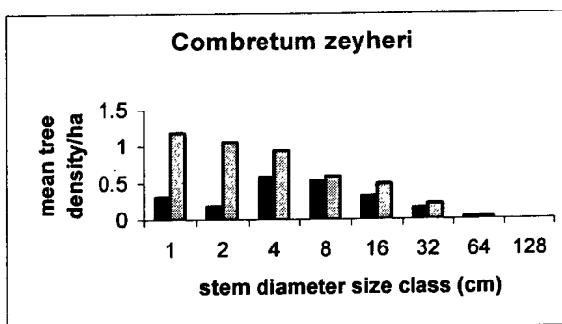
Population Structure

Basal diameter was considered to be the most appropriate single measure of tree age as height may be modified through herbivory, harvesting, fire or competition with other plants for limited resources. Size class profiles for populations in protected areas differed significantly from those in communal rangelands for *D. cinerea* ($p < 0.05$), *P. africanum* ($p < 0.02$), *C. collinum* ($p < 0.05$) and *Diospyros mespiliformis* ($p < 0.02$), and although not significant, other species showed trends in population structure associated with land use. Species showing size class profiles that differed with land use include: *T. sericea*, *C. zeyheri*, *Combretum hereroense*, *Dalbergia melanoxylon*, *Lannea schweinfurthii* and *S. madagascariensis*, all with an "inverse-J" shaped profile in protected areas and a "humped" profile ("flattened" for *C. hereroense* and *L. schweinfurthii*) in communal lands (Figures 2a-e), suggesting either a suppression of recruitment or episodic/pulsed recruitment. *S. madagascariensis*, *Diospyros mespiliformis* and *P. africanum* showed the reverse with an "inverse-J" profile in communal lands and a "humped"/"flattened" profile in protected areas (Figures 2f-h).

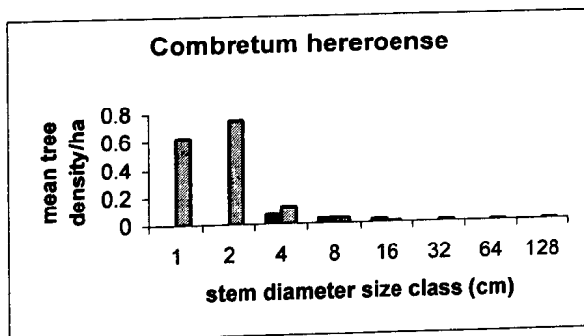
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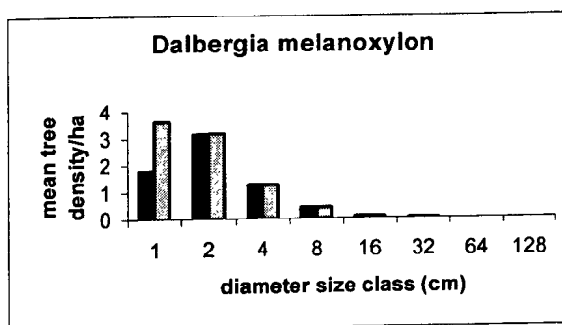
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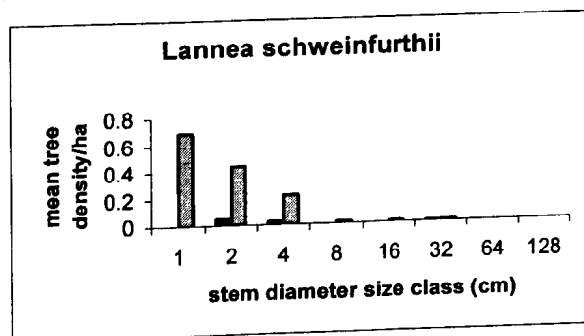
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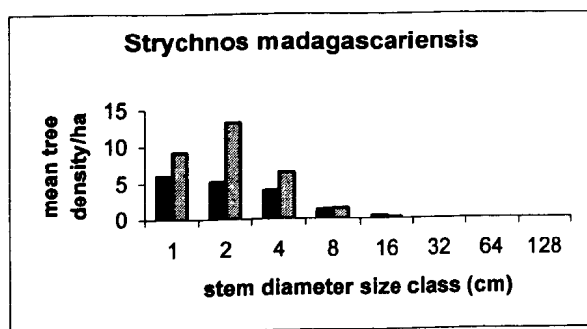
(e)



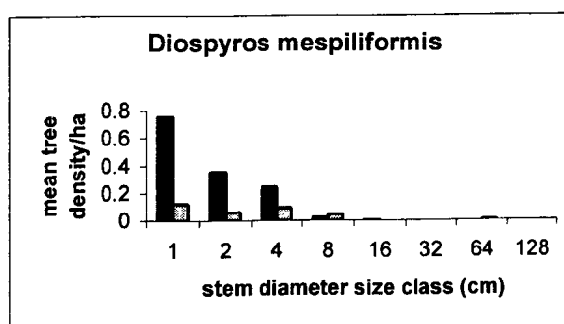
communal 
Protected 

Figure 2. Size class profiles (based on basal stem diameters) for species with differences in population structure according to land use.

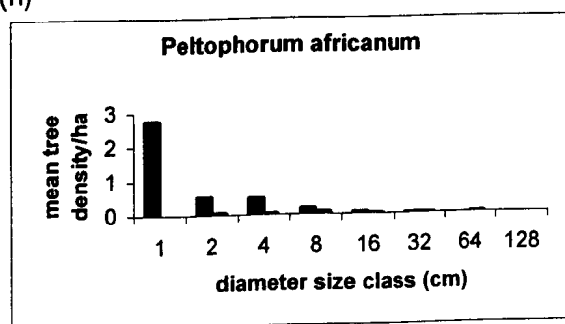
(f)



(g)



(h)

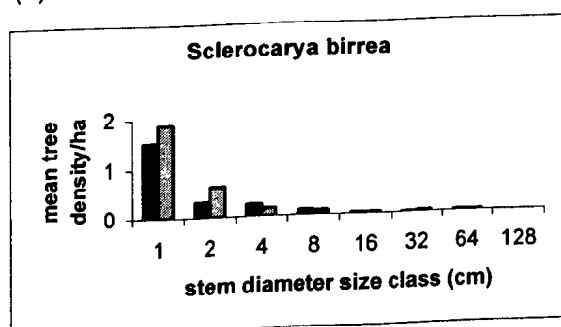


communal 
Protected 

Figure 2., continued. Size class profiles (based on basal stem diameters) for species with differences in population structure according to land use.

Species showing similar "inverse-J"-shaped size class profiles under both land uses include *Sclerocarya birrea* and *Lonchocarpus capassa* (Figures 3a,b). In communal lands, both show a reduced frequency of individuals within intermediate diameter size classes compared with populations sampled within adjacent protected areas.

3(a)



(b)

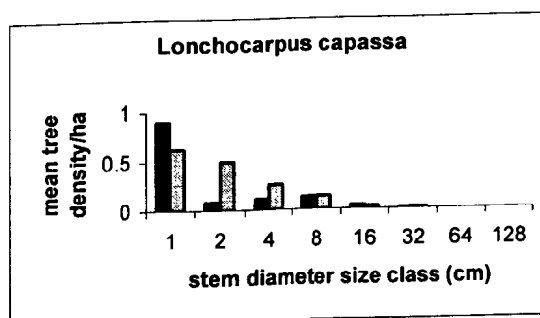
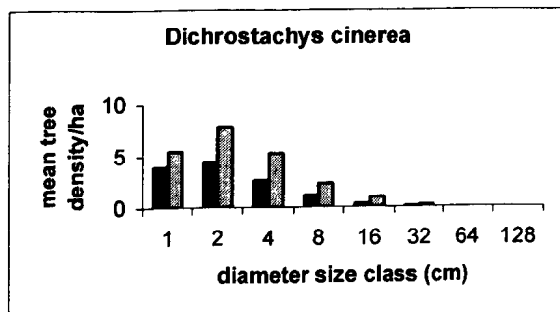


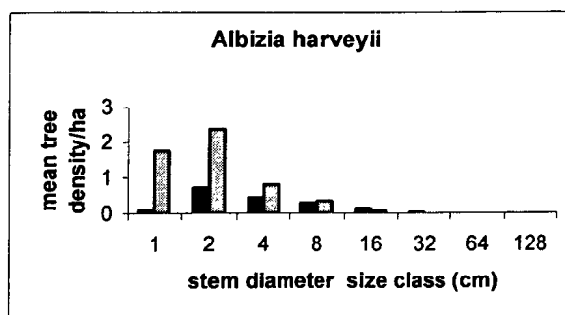
Figure 3. Size class profiles (based on basal stem diameters) for species that show little differences in population structure with land use.

Species showing similar “hump”-shaped size class profiles under both land uses include (Figures 4a-d): *D. cinerea*; *Albizia harveyi*; *C. collinum* and *C. apiculatum*, all having higher numbers of individuals per size class in protected areas. *Ziziphus mucronata* has a higher number of individuals per size class in communal areas (Figure 4e).

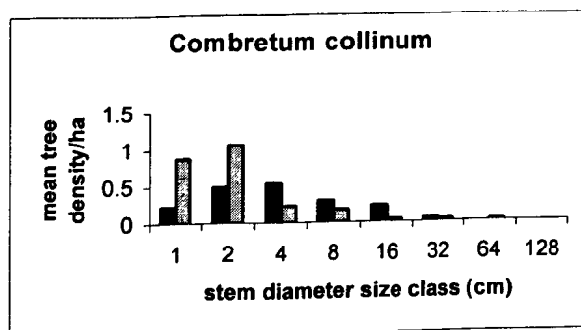
4(a)



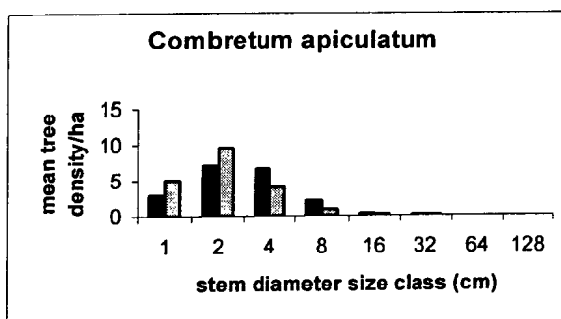
(b)



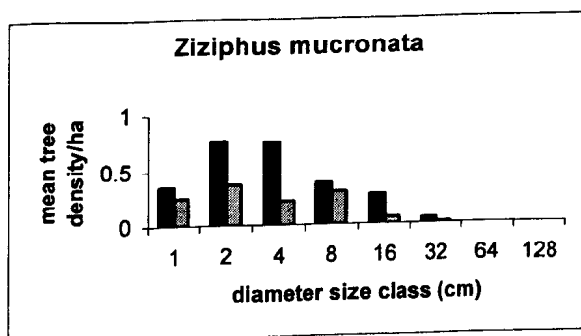
(c)



(d)



(e)



communal 
protected 

Figure 4. Size class profiles (based on basal stem diameters) for species that show similar “hump-shaped” size class distributions with land use.

Recruits and Adults

As an indication of recruitment potential the relative proportion of “recruits” and “adults” of the sampled population was compared between land uses. Recruits were defined as stems (either seedlings or resprouts) with a basal diameter less than 1 cm whilst an adult was an individual exceeding a height of $1/3 \times \text{mean of 10 tallest sampled individuals of that species}$ (pers. obs. and Shackleton 1997)). Here height was considered to be more important than diameter in determining whether an individual was reproductively mature and able to produce seeds as individuals whose height has been reduced through harvesting are likely to remain in a vegetative phase even though their diameter may reflect that they are relatively old.

There was no significant difference in recruits between land uses. *T. sericea*, *D. cinerea*, *S. birrea*, *L. capassa* and *C. zeyheri* had fewer adults within communal lands. *T. sericea* and *D. cinerea*, favoured for construction and fuel wood, had ten and nine times fewer adults respectively in communal areas than in adjacent protected areas.

Morphology

Most species showed a significant effect of land use on both mean stem diameter and height (Tables 3 & 4). A “mean” tree was significantly taller and bigger in diameter in protected areas. Species significantly taller and having a larger mean diameter in protected areas were *D. cinerea*, *P. africanum*, *C. collinum*, *D. mespiliformis* and *T. sericea*. Species with a larger mean height and diameter in communal lands include *L. schweinfurthii*, *A. harveyi*, *S. madagascariensis* and *C. hereroense*. *C. zeyheri* and *S. birrea* had a larger mean height in communal lands; *L. capassa* in protected areas, without significantly differing in mean diameter with land use. *Z. mucronata* showed no significant difference in height or diameter with land use. Regression analyses showed that height and diameter are highly correlated for either land use, but that trees of the same diameter are taller in protected areas in contrast with those in communal areas. Exploring the degree of multi-stemmedness in relation to land use: *T. sericea* is exceptional in that the number of stems per plant unit is significantly ($p < 0.002$) greater in communal lands than in protected lands (nearly double) even though there are more trees in protected areas, indicating that *T. sericea* is a vigorous resprouter. Similarly *C. hereroense* has a third more stems per plant unit in communal lands.

6. DISCUSSION & CONCLUSIONS

The high level of variability between sites within both communal lands and protected areas (probably indicative of both patchily-distributed species and differences in site history/management) may be masking differences in species' density and population structure. Land use alone, therefore, cannot be used to explain differences in densities. Yet, for many species, and especially those favoured for firewood (e.g. *D. cinerea* and *T. sericea*), there are clearly lower densities within communal lands together and no evidence of bush encroachment.

Two thirds of the species examined had fewer individuals within the smallest diameter size classes within communal rangelands when compared with populations in protected areas. Some of these (*T. sericea*, *D. cinerea* and *C. zeyheri*) also had fewer “adults” within communal lands, possibly indicating a lowered recruitment capacity. These are species that could be considered “sensitive” and/or being targeted by harvesting (or other disturbances associated with communal lands). Other species (*C. apiculatum* and *Z. mucronata*) may be episodic recruiters, showing low recruitment in both communal and protected lands. *S. birrea* and *L. capassa* show recruitment in both communal and protected areas (the “inverse-J” shaped curves indicative of regular recruitment). In communal lands, however, the intermediate size classes have fewer individuals. It remains to be determined what is preventing individuals from growing into these intermediate diameter size classes.

In contrast to the lack of obvious population level differences with land use, there were highly significant differences in individual plant morphology (with the exception of *Z. mucronata*): the “mean tree” in communal lands is smaller: shorter, of smaller stem diameter and has more stems per tree unit. Individuals of the majority of the species examined were stunted both in height and diameter, limited in size probably both through harvesting and livestock browsing damage. Plants in communal lands may be persisting, resprouting following harvesting and browsing damage. All species selected for this study were able to resprout, although with highly variable vigour, dependent on both species and size (unpubl. data) and it is not known how much disturbance (with what frequency and intensity) they can survive. Stunted individuals produce fewer seeds, which in the future is likely to translate into compositional changes.

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Table 1. Mean tree density/ha⁻¹ for selected savanna woody plants in Communal vs Protected areas

<i>Species</i>	<i>Mean Tree Density/ha⁻¹ (communal)</i>	<i>SE</i>	<i>n</i>	<i>Mean Tree Density/ha⁻¹ (protected)</i>	<i>SE</i>	<i>n</i>	<i>P</i>
DICI	218.8	64.4	1531	382.8	201.5	463	> 0.1
PEAF	66.2	37.9	463	10.9	6.2	54	> 0.1
DAME	101.7	52.1	712	95.7	38	478	> 0.1
LASC	2.3	1.3	16	19.1	6.3	96	> 0.1*
ALHA	47	23.1	329	53.3	31.3	266	> 0.1
LOCA	24.1	10.7	168	28.3	10.6	141	> 0.1
SCBI	39.7	14.5	278	39.6	9.4	198	> 0.1
ZIMU	72.4	43.1	507	24.7	9.4	123	> 0.1
STMA	275.1	97.5	1926	412.3	224	2061	> 0.1
COCO	55.7	48.7	390	26.9	25.7	134	> 0.1
COAP	358.4	190.3	2509	294.4	135.2	1472	> 0.1
COHE	5.6	3.2	35	20.8	19.1	104	> 0.1
COZE	100.8	42.3	706	172	51.1	858	> 0.1**
DIME	18.5	13.7	130	5.25	2.65	26	> 0.1
TESE	275	100.4	1925	355.8	151.4	1779	> 0.1
ALL	1660.5	138.5	11624	1925.9	193.4	9706	> 0.1

ALHA - Albizia harveyi
COAP - Combretum apiculatum
COCO - Combretum collinum
COHE - Combretum hereroense
COZE - Combretum zeyheri
DAME - Dalbergia melanoxylon
DICI - Dichrostachys cinerea
DIME - Diospyros mespiliformis

LASC - Lannea schweinfurthii
LOCA - Lonchocarpus capassa
PEAF - Peltophorum africanum
SCBI - Sclerocarya birrea
STMA - Strychnos madagascariensis
TESE - Terminalia sericea
ZIMU - Ziziphus mucronata

* SAS analyses found a significant difference in LASC tree density between land uses; but small sample sizes

** Paired t-test: COZE significant ($P < 0.05$; $P=0.027$) difference in number of trees between Communal and Protected, but SAS taking account of variance found the difference to be non-significant.

Table 2. Mean stem density/ha⁻¹ for selected savanna woody plants in Communal vs Protected areas

<i>Species</i>	<i>Mean Stem Density/ha⁻¹ (communal)</i>			<i>Mean Stem Density/ha⁻¹ (protected)</i>			<i>P</i>
	<i>SE</i>	<i>n</i>		<i>SE</i>	<i>n</i>		
DICI	630	207.9	4410	882.7	475.7	4413	> 0.1
PEAF	108	49.7	756	31.3	14.7	156	> 0.1
DAME	179	92.7	1252	160.6	67.2	803	> 0.1
LASC	3.2	1.9	23	26.6	8.8	133	> 0.1
ALHA	129	74.6	904	159.3	79.3	796	> 0.1
LOCA	51	20.9	357	55.7	21.4	278	> 0.1
SCBI	66	28.7	461	50.9	15.2	1074	> 0.1
ZIMU	153	99.6	1074	55.1	18.8	275	> 0.1
STMA	1071.9	467.8	7503	1487.8	724.1	7439	> 0.1
COCO	161	124	1128	63.2	54.2	316	> 0.1
COAP	747	387.1	5229	538.5	224	2693	> 0.1
COHE	15.6	7.7	93	43.9	35.4	219	> 0.1
COZE	486.5	186	3406	823.3	237.6	4142	> 0.1*
DIME	25.7	17.4	180	9.44	4.1	47	> 0.1
TESE	1022.5	414.1	7158	696.6	547.2	3483	> 0.1
ALL	4456.3	410.4	33933	5089.8	702	25449	> 0.1

ALHA - *Albizia harveyi*
COAP - *Combretum apiculatum*
COCO - *Combretum collinum*
COHE - *Combretum hereroense*
COZE - *Combretum zeyheri*
DAME - *Dalbergia melanoxylon*
DICI - *Dichrostachys cinerea*
DIME - *Diospyros mespiliformis*

LASC - *Lannea schweinfurthii*
LOCA - *Lonchocarpus capassa*
PEAF - *Peltophorum africanum*
SCBI - *Sclerocarya birrea*
STMA - *Strychnos madagascariensis*
TESE - *Terminalia sericea*
ZIMU - *Ziziphus mucronata*

* Paired t-test: COZE significant ($P < 0.05$; $P=0.03$) difference in number of stems between Communal and Protected; SAS accounting for variance found the difference to be non-significant.

Table 3. Mean diameter (cm) for selected savanna woody plants in Communal vs Protected areas.

<i>Species</i>	<i>Mean Tree</i>			<i>Mean Tree</i>		
	<i>Diameter</i> <i>(communal)</i>	<i>SE</i>	<i>n</i>	<i>Diameter</i> <i>(protected)</i>	<i>SE</i>	<i>n</i>
DICI	4.81	0.26	483	8.66*	0.33	855
PEAF	7.63	1.19	146	42.23*	2.22	73
DAME	9.05*	0.77	285	8.86	0.77	260
LASC	24.48*	2.4	32	15.04	2.15	53
ALHA	12.37*	1.09	133	6.87	0.72	154
LOCA	11.35	1.46	77	16.12	2.33	75
SCBI	31.61	1.24	281	29.39	1.28	241
ZIMU	12.54	0.49	305	13.84	0.99	127
STMA	6.21*	0.47	649	3.21	0.2	698
COCO	14.75	1.43	197	29.16*	1.85	188
COAP	12.19	0.46	1105	14.19*	0.56	837
COHE	22.98*	3.17	27	16.69	2.95	56
COZE	24.20	0.78	474	24.79	0.8	534
DIME	13.19	3.52	50	33.61*	4.99	32
TESE	8.94	0.34	701	12.05*	0.27	1408
ALL	12.44	0.22	4949	13.76*	0.22	5580

* - significant difference ($P < 0.05$)

ALHA - Albizia harveyi
COAP - Combretum apiculatum
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SCBI - Sclerocarya birrea
STMA - Strychnos madagascariensis
TESE - Terminalia sericea
ZIMU - Ziziphus mucronata

Table 4. Mean height (m) for selected savanna woody plants in Communal vs Protected areas.

Species	Mean Tree			Mean Tree		
	Height (communal)	SE	n	Height (protected)	SE	n
2.1.1 DICI	1.31	0.04	485	2.50*	0.06	858
PEAF	1.14	0.13	146	5.06*	0.16	73
DAME	2.67*	0.16	285	2.42	0.13	260
LASC	6.63*	0.44	32	3.53	0.42	52
ALHA	2.92*	0.22	134	1.92	0.17	154
LOCA	2.55	0.31	77	3.46*	0.36	70
SCBI	6.28*	0.22	281	5.72	0.20	241
ZIMU	4.35	0.12	304	4.23	0.17	126
STMA	1.16*	0.06	646	0.79	0.03	698
COCO	3.80	0.12	197	4.58*	0.19	190
COAP	3.40	0.08	1104	3.49*	0.09	831
COHE	4.29*	0.34	28	3.19	0.3	57
COZE	4.31*	0.07	471	3.90	0.08	527
DIME	2.07	0.39	50	5.18*	0.52	32
TESE	2.33	0.07	699	4.10*	0.06	1393
ALL	2.96	0.04	4936	3.29*	0.03	5562

* - significant difference ($P < 0.05$)

ALHA - Albizia harveyi
COAP - Combretum apiculatum
COCO - Combretum collinum
COHE - Combretum hereroense
COZE - Combretum zeyheri
DAME - Dalbergia melanoxylon
DICI - Dichrostachys cinerea
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LASC - Lannea schweinfurthii
LOCA - Lonchocarpus capassa
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SCBI - Sclerocarya birrea
STMA - Strychnos madagascariensis
TESE - Terminalia sericea
ZIMU - Ziziphus mucronata

2.1.2 APPENDIX

Dominant and economically-important savanna woody plant species selected for investigation

- *Combretum apiculatum* (red bushwillow)
- *Combretum collinum* (variable bushwillow)
- *Combretum zeyheri* (large-fruited bushwillow)
- *Combretum hereroense* (russet bushwillow)
- *Terminalia sericea* (silver clusterleaf)
- *Sclerocarya birrea* (marula)
- *Lannea schweinfurthii* (false marula)
- *Diospyros mespiliformis* (jackalberry)
- *Strychnos madagascariensis* (black monkey orange)
- *Lonchocarpus capassa* (apple leaf)
- *Ziziphus mucronata* (buffalo thorn)
- *Dalbergia melanoxylon* (zebrawood)
- *Dichrostachys cinerea* (sickle bush)
- *Albizia harveyi* (sickle-leaved albizia)
- *Peltophorum africanum* (weeping wattle)

APPENDIX 2. Scientific, family and common names of the study species. Nomenclature according to conventions used in Germishuizen & Meyer (Eds.) (2003). General description of growth form from Van Wyk (1990).

SPECIES	FAMILY	COMMON NAME	GROWTH FORM
• <i>Albizia harveyi</i> E. Fourn.	Fabaceae	Common false thorn	ss/ms, medium tree
• <i>Combretum apiculatum</i> Sond. subsp. apiculatum	Combretaceae	Red bushwillow	ss/ms, medium tree
• <i>Combretum collinum</i> Fresen. subsp. gazense Swynn & Baker. f.	Combretaceae	Variable bushwillow	ss/ms, medium tree
• <i>Combretum hereroense</i> Schinz var. villosissimum Engl. & Diels	Combretaceae	Large-fruited bushwillow	ss/ms, medium tree
• <i>Dalbergia melanoxylon</i> Guill. & Perr.	Fabaceae	Zebrawood	ss/ms, medium tree
• <i>Dichrostachys cinerea</i> (L.) Wight & Arn. subsp. Africana	Mimosoideae	Sicklebush	ms, small tree
• <i>Diospyros mespiliformis</i> Hochst. ex A.DC.	Ebenaceae	Jackalberry	ss, large tree
• <i>Lannea schweinfurthii</i> (Engl.) Engl. var. Stuhlmanni	Anacardiaceae	False marula	ss, large tree
• <i>Lonchocarpus capassa</i> Rolfe (= <i>Philenoptera violacea</i> (Klotzsch) Schrire	Fabaceae	Apple leaf	ss, medium tree
• <i>Peltophorum africanum</i> Sond.	Fabaceae	Weeping wattle	ms, medium tree
• <i>Sclerocarya birrea</i> (A. Rich.) Hochst. subsp. Caffra (Sond.) kokwaro	Anacardiaceae	Marula	ss, large tree
• <i>Strychnos madagascariensis</i> Poir.	Loganiaceae	Back monkey orange	ms, medium tree
• <i>Terminalia sericea</i> Burch. ex DC.	Combretaceae	Silver clusterleaf	ss, medium tree
• <i>Ziziphus mucronata</i> Willd. subsp. mucronata	Rhamnaceae	Buffalo thorn	ss, small tree

Growth Form Abbreviations: ss: single-stemmed; ms: multi-stemmed.

References

Germishuizen, G. and Meyer, N. L. (Eds.). 2003. *Plants of Southern Africa: an annotated checklist. Strelitzia 14.*, National Botanical Institute, Pretoria.
 Van Wyk, P., 1990. *Piet Van Wyk's field guide to the trees of the Kruger National Park.* (3rd Edition). C. Struik Publishers, Cape Town.

APPENDIX 3. Herbaceous cover along a gradient of rangeland utilisation intensity.

Grass biomass was calculated for three plots at three sampling distances from Thorndale settlement, and for three plots in the adjacent Manyeleti protected area. Live wood biomass and woody plant population structure were recorded in the same plots (Chapter 2). Using a disc pasture meter, grass biomass was measured at fifty points (three steps apart) parallel to the plot and a further fifty perpendicular to the plot, giving a total of 100 points per plot. Following Bransby & Tainton (1977), grass biomass was calculated as:

$$\text{Grass biomass (kg h}^{-1}\text{)} = 340 + 388.3 \times \text{mean disc height (cm)}$$

The dominant grass species were identified at each point and their relative prevalence (aerial cover) at each sampling distance determined. Grass species were categorised (i) functionally as either decreasers (dominating rangelands in good condition but decreasing when mismanaged), increaser I (dominating poor rangeland and increasing with understocking) or increaser II species (increasing with moderate to severe overgrazing), and (ii) according to perenniality (Tainton 1981, Van Oudtshoorn 1999) (Appendix 3, Table 1).

Grass biomass increased with distance from Thorndale village (ANOVA: $F_{2,897} = 46.73$; $P = 4.95e^{-20}$) and was higher in the Manyeleti protected area than in the communal land sites furthest from the village ($F_{2,598} = 311.9$; $P = 1.75e^{-56}$). The composition of dominant grass species changed with distance from the village. The largest proportion of decreasers were found furthest from the village, whereas that of increaser II species was found close to the village under heavy livestock (goats and cattle) grazing pressure. Annual or weakly perennial species (particularly *Urochloa mosambicensis*) predominated close to the settlement, with a higher proportion of perennial grasses (mostly *Panicum maximum*) at sites further away. *Chloris virgata*, was prevalent in the protected area site, perhaps indicating a seasonal pan.

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- Van Oudtshoorn, F., 1999. *Guide to Grasses of Southern Africa*. Briza Publications, Pretoria.

APPENDIX 3. Table 1. Mean grass biomass $\pm$ SD (kg ha⁻¹) and percentage relative dominance of grass species (based on aerial cover) for sites at different distances from Thorndale settlement and for the adjacent Manyeleti protected area. Dominant grass species were classified into (i) functional categories of decrease and increase species, and (ii) according to perenniality, and relative dominance was summarised.

Grass Species	Functional Category	Perenniality	Distance from settlement			
			Near (n = 300)	Mid (n = 300)	Far (n = 300)	Protected (n = 300)
			1419.5 ± 505.9	1503.6 ± 574.3	2010.3 ± 1175.1	4065.7 ± 1638
			Relative Dominance (%)			
<i>Aristida congesta</i>	increaser II	weak perennial tufted	12.0	5.7	6.7	0.3
<i>Chloris virgata</i>	increaser II	weak perennial tufted	0.0	0.0	0.0	55.5
<i>Eragrostis rigidior</i>	increaser II	annual/weak perennial tufted	3.7	0.3	2.7	1.7
<i>Urochloa mosambicensis</i>	increaser II	weak perennial tufted	52.2	18.2	23.3	3.0
<i>Eragrostis gummiflua</i>	increaser II	perennial tufted	5.0	0.0	0.7	0.0
<i>Heteropogon contortus</i>	increaser II	perennial tufted	0.0	0.0	0.3	1.0
<i>Dactyloctenium australe</i>	increaser II	creeping	0.0	0.0	0.0	2.4
<i>Melinis repens</i>	increaser II	weak perennial tufted	0.0	0.3	0.0	0.0
<i>Panicum ecklonii</i>	decreaser	perennial tufted	1.0	2.0	2.3	1.4
<i>Panicum maximum</i>	decreaser	perennial tufted	4.0	38.9	46.7	34.4
<i>Perotis patens</i>	increaser II	annual/weak perennial tufted	10.7	14.2	0.3	0.0
<i>Pogonarthria squarrosa</i>	increaser II	weak perennial tufted	11.4	18.6	10.0	0.3
<i>Themeda triandra</i>	decreaser	perennial tufted	0.0	1.8	7.0	0.0
Total decreaser			5.0	42.7	56.0	35.8
Total increaser II			95.0	57.3	44.0	64.2

APPENDIX 4. Influence of land use on the relationship between woody plant height and stem diameter, for combined and individual study species: ($\log_{10}(\text{height}) \sim \log_{10}(\text{diameter}) + \text{land use}$) (Bold P < 0.05).

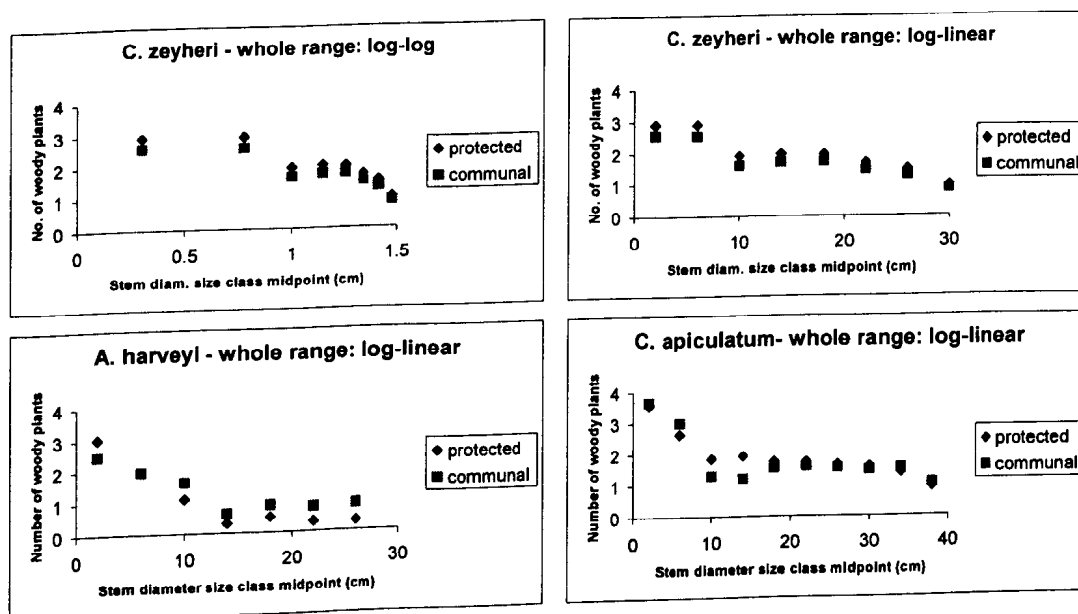
Species: $\log_{10}(\text{height})$	intercept $\pm$ SE	$\log_{10}(\text{diameter}) \pm$ SE	land use $\pm$ SE **	F	R	P
ALL species	-0.26 $\pm$ 0.004	0.792 $\pm$ 0.004	0.027 $\pm$ 0.004	$F_{2,9250} = 24000$	0.84	< 0.0001
<i>A. harveyi</i>	-	-	-	-	-	0.8
<i>C. apiculatum</i>	-0.112 $\pm$ 0.006	0.709 $\pm$ 0.006	-0.025 $\pm$ 0.007	$F_{2,1854} = 6300$	0.87	< 0.0001
<i>C. collinum</i>	-0.05 $\pm$ 0.023	0.675 $\pm$ 0.022	-0.089 $\pm$ 0.024	$F_{2,263} = 464.3$	0.78	< 0.0001
<i>C. zeyheri</i>	-0.075 $\pm$ 0.012	0.634 $\pm$ 0.01	-0.024 $\pm$ 0.008	$F_{2,895} = 1968$	0.82	< 0.0001
<i>D. cinerea</i>	-0.279 $\pm$ 0.012	0.782 $\pm$ 0.013	0.09 $\pm$ 0.013	$F_{2,1176} = 2050$	0.77	< 0.0001
<i>D. melanoxylon</i>	-0.195 $\pm$ 0.014	0.755 $\pm$ 0.015	-0.044 $\pm$ 0.018	$F_{2,455} = 1299$	0.85	0.01
<i>L. capassa</i>	-0.408 $\pm$ 0.028	0.80 $\pm$ 0.025	0.075 $\pm$ 0.035	$F_{2,135} = 537$	0.89	0.03
<i>S. birrea</i>	-	-	-	-	-	0.1
<i>S. madagascariensis</i>	-	-	-	-	-	0.8
<i>T. sericea</i>	-0.288 $\pm$ 0.009	0.772 $\pm$ 0.008	0.143 $\pm$ 0.009	$F_{2,1628} = 5683$	0.87	< 0.0001
<i>Z. mucronata</i>	-0.048 $\pm$ 0.021	0.69 $\pm$ 0.021	-0.052 $\pm$ 0.018	$F_{2,395} = 564$	0.74	< 0.0001

**** where the coefficient of land use is positive, protected areas have taller woody plants than communal rangelands; when negative woody plants are generally taller in communal rangelands than in protected areas**

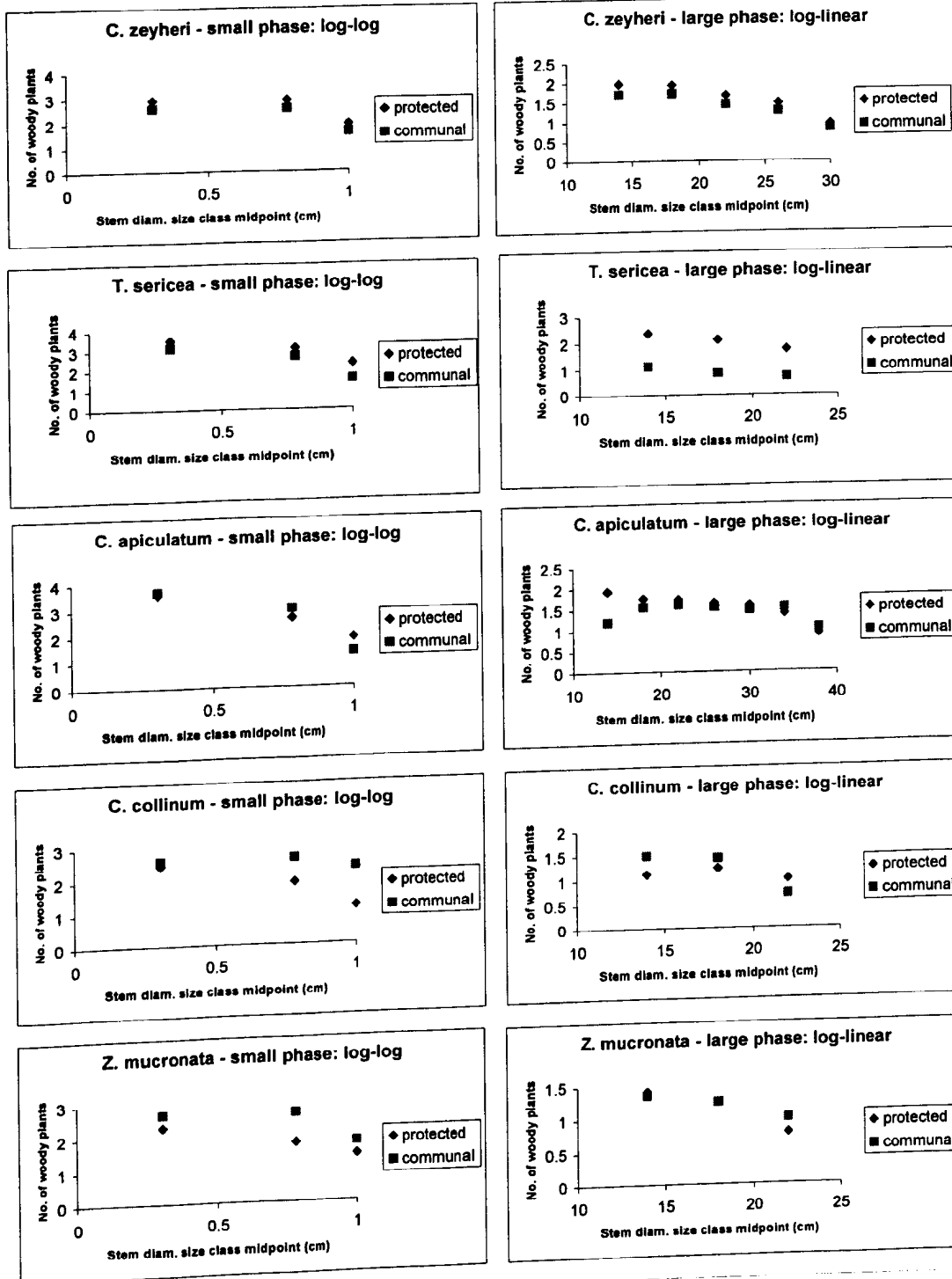
APPENDIX 5. Woody plant population structure and descriptive functions.

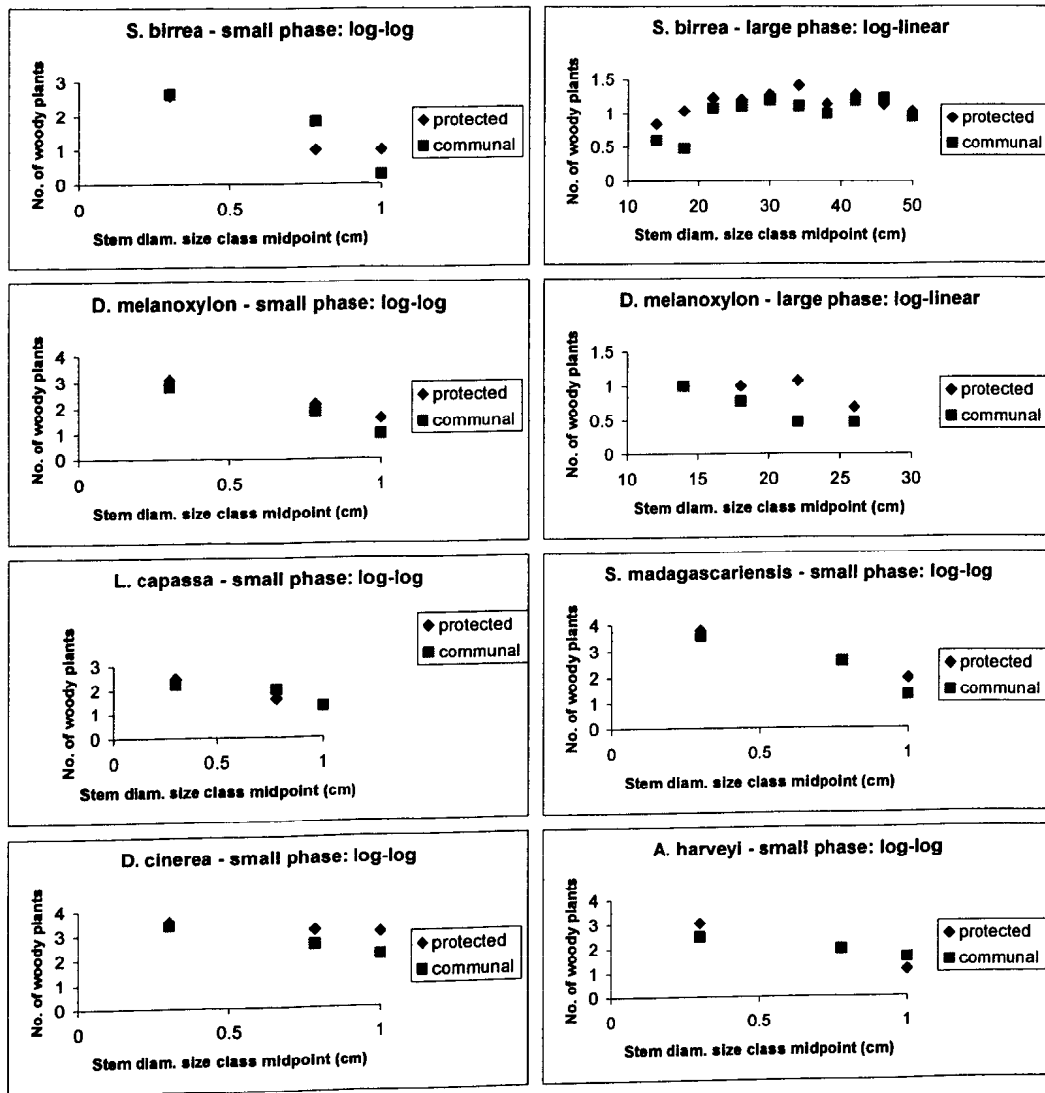
Following Coomes *et al.* (2003), stem diameter size class distributions were additionally represented by plotting the number of woody plants per size class against size class midpoint. Provided growth rate is constant in all size classes, size frequency distributions plotted on log-log axes can be represented as 'straight lines' if the relationships are described by scaling functions (e.g. the size frequency distributions of natural forests were proposed by Enquist & Niklas (2001) to scale as the -2 power of stem diameter); the same size frequency distributions plotted on log-linear axes appear as straight lines if the relationships are negative exponential (Coomes *et al.* 2003). An exponential (log) decline in the number of woody plants with increasing size is explained by a constant attrition rate, assuming a constant time relationship along the x-axis. As in Coomes *et al.* (2003), woody plants were divided into a 'small' and 'large' plant phase (stem diameter ≤ 12 cm and stem diameter > 12 cm, respectively) and plotted on log-log and log-linear axes (logs are base 10) respectively, to assess whether scaling and negative exponential functions could be used to describe each phase. The distinction between plant phases was based on a clear inflection point that occurred in the 10 to 14 cm stem diameter size class for all species when their entire stem diameter range was plotted. Size classes representing the largest plants with fewer than five individuals were pooled. Four of the study species had relatively few woody plants of a large size and therefore only plots for the small-phase were made.

Size class distributions, for the entire stem diameter range, of three of the study species. An inflection point between a small and a large plant phase can be discerned. For *Combretum zeyheri*, the size class distribution, plotted against both a $\log_{10}$ and a linear X-axis, is shown (X = stem diameter size class midpoint).



The small and large plant phase of each species, plotted separately on log-log axes and log-linear axes, respectively.





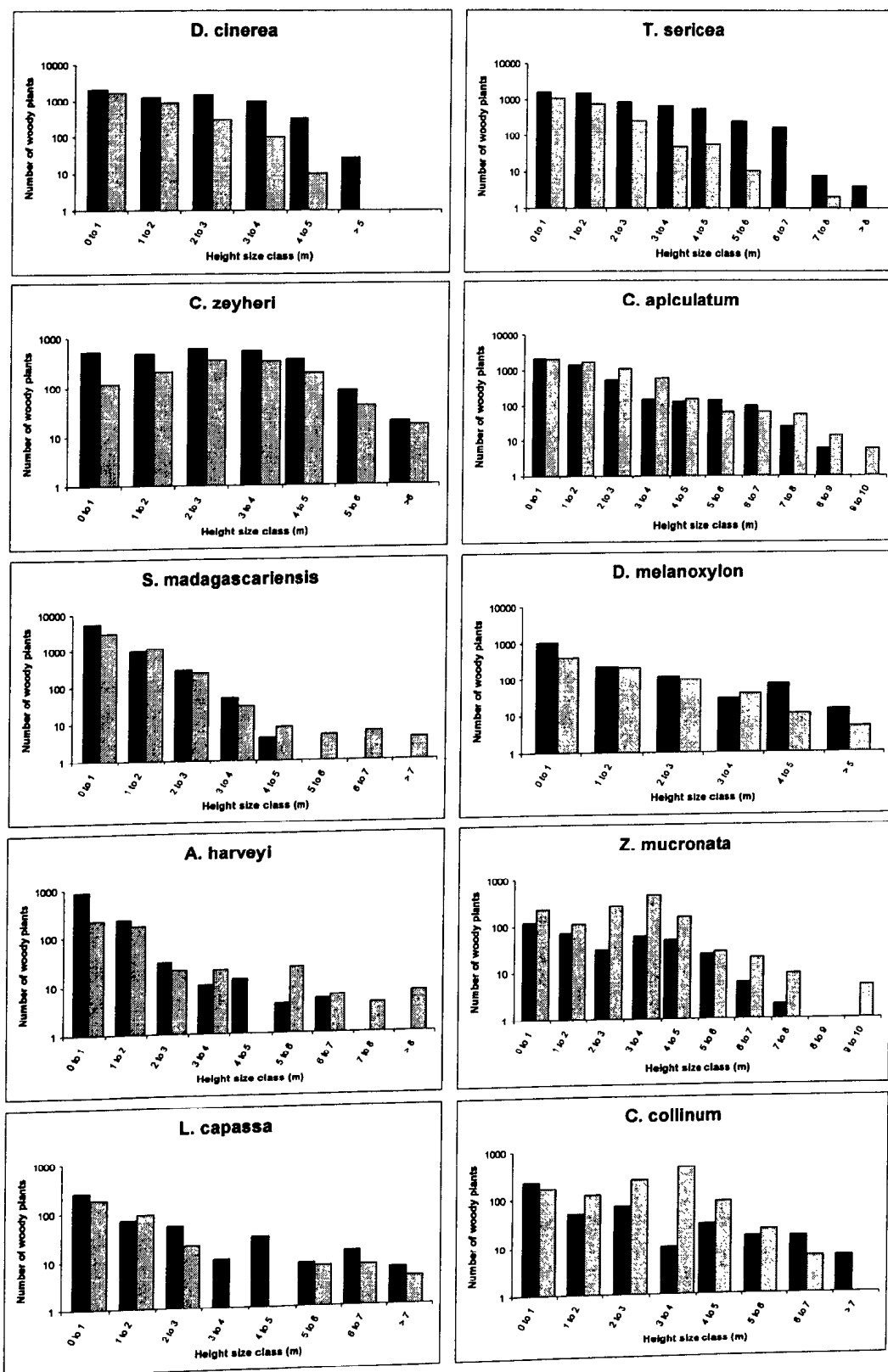
As described by Coomes *et al.* (2003), neither a scaling nor negative exponential function adequately described the entire stem diameter range of the study species. There was an obvious inflection point that was used to distinguish between a 'small' and 'large' plant phase. However, even when the size distributions representing the two plant phases were plotted separately, they were for many species not linearised by either log-log or log-linear axes. The size distributions of *Sclerocarya birrea* showed the greatest departure from linearity. The small plant phase size distributions of a few of the study species, e.g. *Dichrostachys cinerea*; *Dalbergia melanoxylon*; *Strychnos madagascariensis* and *Albizia harveyi*, when plotted on log-log axes appeared relatively straight and were more effectively described by scaling functions.

In agreement with the conclusions drawn by Coomes *et al.* (2003) for tropical rain forest species, the shape of size class distributions appears to be influenced by different agents operating at different life history stages. Neither competition nor a scarcity of limited resources, nor exogenous disturbances can be forwarded as being solely responsible for shaping population structure. During the small plant phase, a high rate of mortality and attenuation in woody plant numbers and a non-constant growth through size classes may result in this trend, whilst a slowing of growth and perhaps a clear senescent-phase may be an explanation for the large plant phase.

References

- Coomes, D. A., Duncan, R. P., Allen, R. B. and Truscot, J., 2003. Disturbances prevent stem size-density distributions in natural forests from following scaling relationships. *Ecology Letters*, 6: 980-989.
- Enquist, B. J. and Niklas, K. J., 2001. Invariant scaling relation across tree-dominated communities. *Nature*, 410: 655-660

APPENDIX 6. Woody plant height distribution within protected areas and adjacent communal rangelands (Chapter 3 contains the height distribution graph for *S. birrea*). Black bars represent protected areas; Grey bars represent communal rangelands.



**APPENDIX 7. Species composition of the harvested study site,
in order of % relative abundance (sample size in parentheses).**

Species	% relative abundance	Sample size
<i>Dichrostachys cinerea</i>	22.5	(216)
<i>Terminalia sericea</i>	14.2	(136)
<i>Strychnos spinosa</i>	11.7	(112)
<i>Combretum zeyheri</i>	9.3	(89)
<i>Senna petersiana</i>	6.6	(63)
<i>Strychnos madagascariensis</i>	6.1	(59)
<i>Pterocarpus rotundifolius</i>	4.9	(47)
<i>Combretum collinum</i>	3.1	(33)
<i>Euclea natalensis</i>	2.3	(22)
<i>Pavetta gardeniifolia</i>	2.1	(20)
<i>Ehretia obtusifolia</i>	1.8	(17)
<i>Diospyros mespiliformis</i>	1.6	(15)
<i>Flueggia virosa</i>	1.5	(14)
<i>Gymnosporia heterophylla</i>	1.5	(14)
<i>Peltophorum africanum</i>	1.4	(13)
<i>Euclea divinorum</i>	1.0	(10)
<i>Lonchocarpus capassa</i>	0.9	(9)
<i>Catunaregam spinosa</i>	0.8	(8)
<i>Combretum apiculatum</i>	0.7	(7)
<i>Dalbergia melanoxylon</i>	0.5	(5)
<i>Acacia gerrardii</i>	0.5	(5)
<i>Grewia hexamita</i>	0.5	(5)
<i>Sclerocarya birrea</i>	0.4	(4)
<i>Ziziphus mucronata</i>	0.4	(4)
<i>Acacia swazica</i>	0.4	(4)
<i>Grewia flavescens</i>	0.4	(4)
<i>Rhus glauca</i>	0.4	(4)
<i>Parinari curatellifolia</i>	0.3	(3)
<i>Vangueria infausta</i>	0.3	(3)
<i>Albizia harveyi</i>	0.3	(3)
<i>Lannea schweinfurthii</i>	0.2	(2)
<i>Grewia monticola</i>	0.2	(2)
<i>Lannea discolor</i>	0.2	(2)
<i>Albizia versicolor</i>	0.2	(2)
<i>Acacia caffra</i>	0.2	(2)
<i>Acacia nigrescens</i>	0.1	(1)
<i>Ficus sycomorus</i>	0.1	(1)
<i>Bridelia mollis</i>	0.1	(1)

APPENDIX 8. Resprouting response of the dominant woody plant species as indicated by (a) number of resprout stems; (b) composite resprout shoot diameter; (c) resprouting vigour (composite resprout shoot diameter/composite cut diameter) per harvested woody plant (mean $\pm$ SD) by cut stem diameter size class (figure in parentheses is the number of plants sampled).

Species	Family	Resprouting response - (a) number of resprout shoots					Total
		0 to < 1 cm	1 to < 4 cm	4 to < 10 cm	10 to < 20 cm	≥ 20 cm	
<i>Dichrostachys cinerea</i>	Mimosoideae	5.89 $\pm$ 3.52 (9)	7.45 $\pm$ 4.8 (29)	9.51 $\pm$ 3.93 (39)	9.64 $\pm$ 4.7 (28)	-	8.67 $\pm$ 4.49 (105)
<i>Strychnos madagascariensis</i>	Loganiaceae	5.87 $\pm$ 2.75 (15)	5.79 $\pm$ 2.53 (39)	8.69 $\pm$ 4.77 (16)	9.67 $\pm$ 6.21 (12)	40 (1)	7.33 $\pm$ 5.41 (83)
<i>Combretum collinum</i>	Combretaceae	5.33 $\pm$ 1.53 (3)	5.54 $\pm$ 2.03 (13)	7.26 $\pm$ 4.24 (19)	9.78 $\pm$ 4.48 (18)	-	7.58 $\pm$ 4.11 (53)
<i>Combretum zeyheri</i>	Combretaceae	5 $\pm$ 2.35 (5)	5.7 $\pm$ 2.83 (20)	5.25 $\pm$ 3.3 (4)	-	-	5.52 $\pm$ 2.73 (29)
<i>Terminalia sericea</i>	Combretaceae	5.67 $\pm$ 2.02 (12)	5.57 $\pm$ 2.89 (28)	6.39 $\pm$ 2.74 (31)	9.08 $\pm$ 4.29(37)	9.5 $\pm$ 7.06 (6)	7.18 $\pm$ 3.89 (114)
<i>Pterocarpus rotundifolius</i>	Papilionoideae	4.4 $\pm$ 1.67 (5)	4.48 $\pm$ 2.25 (29)	6.53 $\pm$ 2.52 (18)	6.78 $\pm$ 3.58 (32)	14.91 $\pm$ 7.67 (11)	6.84 $\pm$ 4.77 (96)

Species	Family	Resprouting response - (b) total resprout shoot diameter (cm)					Total
		0 to < 1 cm	1 to < 4 cm	4 to < 10 cm	10 to < 20 cm	≥ 20 cm	
<i>Dichrostachys cinerea</i>	Mimosoideae	0.94 $\pm$ 0.52 (9)	1.79 $\pm$ 0.9 (29)	2.39 $\pm$ 1.17 (39)	2.56 $\pm$ 1.83 (28)	-	2.15 $\pm$ 1.35 (105)
<i>Strychnos madagascariensis</i>	Loganiaceae	1.17 $\pm$ 0.47 (15)	1.74 $\pm$ 0.72 (39)	2.65 $\pm$ 2.25 (16)	2.61 $\pm$ 0.93 (12)	4.24 (1)	1.97 $\pm$ 1.3 (83)
<i>Combretum collinum</i>	Combretaceae	1.98 $\pm$ 0.6 (3)	1.39 $\pm$ 0.93 (13)	3.27 $\pm$ 2.32 (19)	3.2 $\pm$ 1.82 (18)	-	2.71 $\pm$ 1.96 (53)
<i>Combretum zeyheri</i>	Combretaceae	1.41 $\pm$ 0.47 (5)	1.83 $\pm$ 0.9 (20)	4 $\pm$ 3.21 (4)	-	-	2.06 $\pm$ 1.53 (29)
<i>Terminalia sericea</i>	Combretaceae	1.22 $\pm$ 0.8 (12)	1.82 $\pm$ 1.36 (28)	3.41 $\pm$ 3.06 (31)	3.38 $\pm$ 2.1 (37)	5.73 $\pm$ 4.51 (6)	2.91 $\pm$ 2.55 (114)
<i>Pterocarpus rotundifolius</i>	Papilionoideae	1.35 $\pm$ 0.48 (5)	1.67 $\pm$ 0.92 (29)	3.16 $\pm$ 3.74 (18)	4.34 $\pm$ 2.98 (32)	6.86 $\pm$ 3.45 (11)	3.42 $\pm$ 3.15 (96)

Species	Family	Resprouting response - (c) resprout vigour (total resprout shoot diameter:total cut stem diameter)					Total
		0 to < 1 cm	1 to < 4 cm	4 to < 10 cm	10 to < 20 cm	≥ 20 cm	
<i>Dichrostachys cinerea</i>	Mimosoideae	3.7 $\pm$ 2.88 (9)	1.14 $\pm$ 0.92 (29)	0.19 $\pm$ 0.34 (39)	0.07 $\pm$ 0.11 (28)	-	0.72 $\pm$ 1.39 (105)
<i>Strychnos madagascariensis</i>	Loganiaceae	3.92 $\pm$ 2.67 (15)	1.78 $\pm$ 2.07 (39)	0.33 $\pm$ 0.6 (16)	0.05 $\pm$ 0.04 (12)	0.11 (1)	1.61 $\pm$ 2.23 (83)
<i>Combretum collinum</i>	Combretaceae	5.78 $\pm$ 1.63 (3)	0.69 $\pm$ 0.9 (13)	0.31 $\pm$ 0.5 (19)	0.07 $\pm$ 0.08 (18)	-	0.63 $\pm$ 1.43 (53)
<i>Combretum zeyheri</i>	Combretaceae	4.82 $\pm$ 2.09 (5)	1.12 $\pm$ 0.89 (20)	0.85 $\pm$ 0.8 (4)	-	-	1.72 $\pm$ 1.82 (29)
<i>Terminalia sericea</i>	Combretaceae	3.04 $\pm$ 3.52 (12)	1.5 $\pm$ 2.4 (28)	0.33 $\pm$ 0.56 (31)	0.09 $\pm$ 0.1 (37)	0.11 $\pm$ 0.17 (6)	0.7 $\pm$ 1.53 (114)
<i>Pterocarpus rotundifolius</i>	Papilionoideae	2.05 $\pm$ 2.53 (5)	0.89 $\pm$ 0.97 (29)	0.32 $\pm$ 0.69 (18)	0.14 $\pm$ 0.22 (32)	0.07 $\pm$ 0.06 (11)	0.62 $\pm$ 1.26 (96)

APPENDIX 9. Calculation of pre- and post-harvest wood biomass for the study site.

WOOD BIOMASS	PRE- (kg)	POST- (kg)	
Initial deadwood	145.68		Estimate of initial harvestable deadwood = 303.5 kg/ha (Shackleton 1997)
Uncut woody plants	8420.78	8420.78	Biomass = 0.035 x stem diameter ² x 2.5 (Netshiluvhi & Scholes 2002)
Cut woody plants	1796.70		
'Regeneration'		1.61	'Regeneration': biomass of seedlings and root suckers
Resprouting		650.31	
Stumps		800.96	Stump biomass: wood density*((pi*((diameter/2) ²)*cut height)/(10 ⁴))
Removed/harvested	1942.38		(mean wood density = 880 kg/m ³ ; mean cut height = 0.7 m)
TOTAL (study site)	10363.16	9873.67	Area sampled = 0.48 ha
TOTAL (ha ⁻¹)	15752.01	15007.98	
'Average' cut woody plant	8.72	7.05	
Resprouting per woody plant		3.16	
Resprouting (ha ⁻¹)		988.48	During the 4 months following harvesting
% of total biomass: resprouting		6.6	
'Regeneration' (ha ⁻¹)		2.45	
Annual deadwood (ha ⁻¹) 'pre-harvest'		267.78	Annual deadwood production est. at 1.7% of live biomass (Shackleton 1997)

References

- Netshiluvhi, T. R. and Scholes, R. J., 2002. Allometry of South African woodland trees. In Seydack, A. H. W., Vorster, T., Vermeulen, W. J. and van der Merwe, I. J. (Eds.). *Multiple use management of natural forests and savanna woodlands: policy refinements and scientific progress*. p 280-291, Proceedings of Natural Forest and Savanna Woodlands Symposium III, Kruger National Park, South Africa. Department of Water Affairs and Forestry, Indigenous Forest Management, Pretoria.
- Shackleton, C. M., 1997. The prediction of woody plant productivity in the savanna biome, South Africa. Unpublished PhD thesis, University of the Witwatersrand, Johannesburg.

APPENDIX 10. Assumptions made in developing the woodland model.

Driving factors and woody plant demography:

- *Grass*: although savanna is composed of grass in addition to woody plants, the model focuses on the woody plant component and does not explicitly simulate grass growth. Woody plants are, however, influenced by grass biomass: directly with competition between seedlings and grass reducing seedling establishment, and indirectly by grass biomass supporting fires (or rodents – Chapter 4). Grass biomass will in turn be affected when woody densities increase and alter fire regimes.
- *Fire*: is not considered a significant factor close to settlements where grass biomass is considerably reduced by grazing livestock. The indirect effect of grass biomass on woody plant dynamics through influencing the incidence of fire and potential fire damage to woody plants has not yet been modelled in detail, although this would make an obvious addition, with woody plants that are burnt by fire perhaps reverting by one size class; a resprouting woody plant that is burnt by a fire would start its recovery over again. Instead a ‘background’ level of mortality was assumed which included mortality from fire, and was more likely for woody plants less than two metres in height and especially for seedlings less than one year in age.
- *Rainfall*: (i) simulated as poor; average or wet (based on defined ranges and simulated data (McNeill *et al.* 1994)); (ii) rainfall in the season previous to the first year of the simulation is fixed to be average, supporting some woody plant growth and reproduction; (iii) the distribution of rainfall events during the wet season is not incorporated although this is likely to be important for seedling establishment; (iv) at the moment there is no effect of a series of bad rainfall years (i.e. droughts that tend to occur over periods of several years) on woody plant condition (‘vital biomass’) and subsequent mortality.
- *Woody plant growth*: (i) woody plants grow in size class increments. Assumptions were made regarding species-specific growth increments (according to estimated longevity, wood density and predicted growth rate), and in the conversion from size class to stem diameter; (ii) woody plants are assumed not to grow (nor stumps to ‘recover’) in years of poor rainfall, whilst the amount of growth during both years of average and above-average rainfall is the same; (iii) assumption that close to the settlement (< 500 m) browsing suppresses the growth of individuals < 1 m in height, i.e. seedlings and saplings, and the recovery of stumps,

during years of average rainfall (no growth in poor rainfall years, and escape browsing during wet years).

- *Seed/Seedling production*: (i) the size at which individual's become reproductive (i.e. 0.58 of their maximum height); (ii) the number of seedlings produced per reproductive woody plant is not influenced by the size of the woody plant (only by the amount of rainfall received); (iii) the distance that seedlings are dispersed from adults is based on field observations of the closest potential parent to recorded seedlings.
- *Recruitment*: (i) seedling regeneration niches: at the moment the modelled landscape is homogenous (except for the superimposed gradient of disturbance) and seedlings can establish in any cell that is empty (assumption that seedlings cannot become established within cells already occupied). Detail could be added as to which cells constituted more favourable sites for seedling recruitment (based on tolerances to shade/grass biomass and soil moisture availability); (ii) assumed that soil characteristics and nutrient availability influence microhabitat niche's but are less important in relation to primary determinants of rainfall, grass cover and human-related disturbance (broad-leaved woodlands growing on nutrient-poor sandy upland soils had been sampled); (iii) no more than a single seedling can establish within a cell; simplifying assumption that competition occurs at the seedling stage and not between established individuals.
- *Tree Growth*: gain in wood biomass is currently based on a constant wood density (presently 0.035), while this thesis reports a large variation among species. This variation could be incorporated by assuming that the parameter used to convert volume ($D^{2.5}$) to woody plant biomass (in tonnes) is linearly dependent on density.
- *Harvesting*: (i) at the moment assuming that harvesting preference increases with woody plant size (could adapt woody plant 'Utility' equation for active selection of intermediate size classes); (ii) assumption of a constant height at which woody plants are cut based on the mean height (Chapter 5).
- *Stumps: ~ Time to Recovery*: (i) the great majority of harvested woody plants resprout; (ii) assumption of the time taken for a stump to recover and resume 'normal woody plant' growth; this recovery time is size-specific and not species-specific, assuming no differences in the ability of (and rate at which) species recover follow harvesting damage (could be adapted according to relative resprouting vigour (Chapter 5), wood density and predicted relative growth rates); (iii) stumps do not change in stem diameter size during the recovery period; (iv) do not contribute to deadwood production; (v) do not have an increased probability of mortality; (vi) are not reproductive.

Other model assumptions:

- *Species composition*: the model can easily be adapted to consider different species or plant functional/response types, e.g. based on their resprouting response to damage; (i) currently it is assumed that there are only three species/functional groupings of woody plants, other less common species could perhaps be incorporated (as in Wiegand *et al.* (1995)) as a “fixed plant environment”, occupying space (cells) according to the combined relative density of these species and remaining unchanged during simulation.
- *The initial population*: (i) the initial population structure was chosen from an exponential function around species-specific mean diameters. An alternative would be to base initial population structure on the population structure of populations in protected areas, considered ‘relatively undisturbed’. However, these may have been influenced by browsing elephant, giraffe, kudu and other indigenous browsers or by fire (ii) an individual’s age is assumed to be the same as its size class, assuming that it has experienced favourable growing conditions (rainfall) during its lifetime up to that point.
- *Harvesting and Deadwood*: (i) assumption that no previous harvesting has occurred in the study area prior to the simulation; and (ii) that there has been an accumulation of deadwood; (iii) deadwood is favoured and collected before any live wood is harvested.
- *For Multi-stemmed individuals*: stem diameter reflects the composite diameter of all stems. The number of stems is taken into consideration only when evaluating the woody plant ‘Utility’ value of an individual: harvesters species-specific preferences, and the assumed effect of the number of times a woody plant has been cut on its degree of branching and value to harvesters.
- *Length of the transect grid*: 3 km (the distance range within which cattle graze and people harvest from the settlement) is assumed to be a sufficiently large area to represent the woodland dynamics and allow predictions for the surrounding area. This will require experimental assessment of alternative grid sizes.
- *Human population growth rate and fuelwood demand*: population growth rates in the study region are likely to be reduced through HIV AIDS induced mortality. Several settlements within the study region (including Thorndale) do not have access to electricity. Access to alternative energy sources is unlikely to reduce the fuelwood demand.

References

- McNeill, L. Brandão, A., Zucchini, W. and Joubert, A., 1994. Interpolation of the daily rainfall model. Water Research Commission No. 305/1/94, Water Research Commission, Pretoria.
<http://134.76.173.220/rainfall/index.html>.

APPENDIX 11. Observations of woody plant dynamics by resident resource users.

Interviews with resource users regarding their understanding and perceptions of the wood resource base have been used effectively to supplement empirical analyses of woody plant population structure. In combination, these methods have been found to provide a good indication of vegetation changes, including the decrease in abundance of certain woody plant species and the probable causes thereof (Shackleton 1993, Lykke 1998). This information is important for formulating management plans for disturbed environments, where vegetation changes are occurring rapidly and management is urgently needed.

Following an initial visit to the village 'nduna' or headman to make arrangements, meetings were held with groups of residents in three settlements within the study region (Wolverdind, Seville and Thorndale). Participatory rural appraisal (PRA) methods were used during group discussions, including landscape mapping and qualitative techniques, e.g. using beans to indicate woody plant densities (currently and in the past) or for ranking species in response to a question. Participant group size ranged from twelve to thirty people. Three of the groups were composed of women inhabitants (n = 17; 22; 30), the dominant collectors of fuelwood. A single PRA group was held with men (n = 12). Participants' ages ranged from 20 to 75 years, with several of the elderly members having lived in the region for most of their lives. All but two elderly participants currently harvested live wood for fuelwood (and for construction, fencing and other uses). Inhabitants were asked about their perceptions and observations of woodland vegetation change, the wood resource base and woody plant regeneration. A single interpreter assisted in all the discussions.

Specifically, the participants of each group were asked about:

- observed vegetation changes: woody plant density and woodland structure (including woody plant growth form)
- which species were felt to be increasing or decreasing in density
- probable causes of changes in woody plant density
- the woody plant species most favoured for fuelwood and construction timber
- changes in wood availability and demand
- observations of where woody plant seedlings are found in the landscape and the species represented
- determinants of seedling survival

- whether species differ in their resprouting ability following harvesting and whether other factors are influential, e.g. plant size and cut height
- Possible solutions to prevent the depletion of wood resources and attitudes towards resource management

There were some differences in the opinions expressed by participants (within and between groups) in their understanding of woodland dynamics and woody plant regeneration. However, broad conclusions could be drawn from the dominant (most frequent) opinions expressed by each group. These were largely in agreement with the study's biological findings.

Perceptions of woodland changes

Resource users expressed a perceived decline in the density of all woody plants species (with the possible exception of *Terminalia sericea*, which two of the four groups felt to be increasing in density). Those explicitly mentioned included the leadwood *Combretum imberbe*, highly valued for its dense wood and previously widespread but now rarely found (this was not selected as one of the study species due to its scarceness within the study region at the start of the study) and the wild teak *Pterocarpus angolensis* (groups 1 & 3), *Acacia nigrescens* and *Albizia harveyi* (groups 2 & 4). The participants of all groups agreed that structurally, woodlands had changed to being composed predominantly of smaller, shorter woody plants with fewer plants of a larger size. Large edible fruit-bearing trees, most noticeably the marula *Sclerocarya birrea*, were highly valued and although some were being cut, they were still relatively common.

Most frequently harvested woody plant species

The woody plant species most favoured for fuelwood were *Combretum apiculatum* and *Dichrostachys cinerea* (all four groups). A single group (group 4 - Thorndale) continued to harvest *C. imberbe* and *A. nigrescens*, both of which are scarce in the woodlands surrounding the other settlements. All four of these woody plant species have dense wood and provide good firewood. The species most frequently mentioned to be used for construction or fence/kraal poles were *T. sericea*, *C. imberbe*, *C. apiculatum*, *Combretum hereroense* and *A. nigrescens*. Participants within each group said that termites did not eat the wood of these species.

Woody plant regeneration

The seedlings most frequently observed were those of *S. birrea* and *Diospyros mespiliformis* (all participants of all groups agreed). Seedlings of *D. cinerea*, *Strychnos madagascariensis*, *T. sericea*, *Peltophorum africanum* and *Ziziphus mucronata* were sometimes encountered.

Participants had not seen the seedlings of *C. apiculatum*, *Combretum zeyheri* and *Lonchocarpus capassa*. Seedlings were mostly observed growing beneath the canopies of larger woody plants (by all 4 groups). The shade provides protection - 'an umbrella' - from the sun (i.e. preventing desiccation). Seedlings frequently grew in ploughed fields (groups 2 & 4). The participants of one group stated that seedlings are able to grow wherever there is water. However, seedlings were considered 'tough' with many seedlings surviving even when there was no rainfall. Fire was felt to be an important cause of seedling mortality by all participants. Although livestock browse woody plant seedlings, many survive. Within all groups, participants had observed goats eating the seedlings of *D. mespiliformis*, *S. birrea* and *Z. mucronata*. Browsed *S. birrea* seedlings were reported to be more likely to die relative to other species. Cattle had frequently been observed to eat *D. cinerea* seedlings.

In addition to the unanimous view that water availability was the most important determinant of seedling survival, the resprouting response of plants was evaluated in terms of their perceived ability to retain water (by all three of the groups of women). Woody plant species were defined as being 'wet' or 'dry' depending on their water retention capacity. Wet species (*Combretum collinum* and *S. birrea*) resprouted more vigorously following harvesting than did dry species (*C. apiculatum*, *C. imberbe* and *D. cinerea*). The species classified as being dry species were those with a noticeably denser wood (and presumably a relatively slower growth rate). All groups reached the same conclusions: larger plants resprouted better than small plants of the same species following cutting (however the largest plants often did not resprout and died); the higher a plant was cut the greater its resprouting response; plants that were cut close to the ground often died; and plants that were cut too frequently died.

Concerns about the wood resource base

Most (96%) participants expressed concern about dwindling wood resources. There was no longer deadwood (which previously had been sufficient to meet fuelwood demands) close to the settlement and increasing distances had to be travelled to find wood. Previously, permission had to be sought from the 'nduna' before cutting a live tree. Live wood harvesting was no longer controlled, with plants of all species and sizes cut. People were cutting trees low down to increase the amount of wood obtained. Consequently, trees were observed to have a reduced resprouting vigour with some dying. Fuelwood demand had increased and external users (people from other settlements or towns) were mostly held responsible for reducing wood resources, apparently cutting large quantities of wood to be sold elsewhere. All participants felt that woodlands needed to be managed, that inhabitants should not be allowed to commercialise wood and that non-

inhabitants should be prevented from cutting wood. There was disagreement over who (local government, traditional authorities, etc.) should be responsible for management. Two groups felt that rotational harvesting strategies could be effective. Several participants suggested protecting harvested plants so that they could have time to recover. Many said that until there were jobs and “money for electricity” there was no way of reducing current levels of harvesting.

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