

The copyright of the above-mentioned described thesis rests with the author or the University to which it was submitted. No portion of the text derived from it may be published without the prior written consent of the author or University (as may be appropriate). *Short quotations may be included in the text of a thesis or dissertation for purposes of illustration, comment or criticism, provided full acknowledgement is made of the source, author and University.*

**THE PREDICTION OF WOODY PRODUCTIVITY IN THE
SAVANNA BIOME, SOUTH AFRICA**

Charles Michael Shackleton

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.

Klaserie, September 1997

ABSTRACT

This thesis reports upon the findings of a four year study into the nature and management of woody plant productivity in the savanna biome, South Africa. The key components were to (1) quantify the range of woody productivity from a variety of sites throughout the biome, (2) seek relationships between the measured productivity and site and environmental variables, and (3) elucidate the impact of selected management actions on woody productivity. Each of these was pursued through a combination of field surveys and empirical experimentation. The basic tenet of the study was to highlight the range of variability and to sample across it, rather than the pursuit of central tendencies and mean responses.

Absolute woody plant productivity, as indexed through mean annual increment in stand basal area at 51 sites over four years, was spatially and temporally variable, ranging from 0.2 m²/ha/yr to 0.65 m²/ha/yr (corrected for death). Significant correlates were rainfall and soil texture. Mean relative woody plant productivity ranged from 2.0 % to 6.4 %. The primary correlate was stand basal area, but a significant relationship was also evident with mean annual rainfall. Whilst most sites indicated an increase in woody basal area from year to year, high mortality rates resulted in 34 % of sites having a net decrease in basal area over the four year period. Stem mortality averaged 4.4 % per year on a density basis. In comparison, seedling recruitment was not prevalent across all sites, but where it was recorded, the number of recruits was considerably higher than required to compensate for mortality. Inter-site recruitment was positively related to rainfall. Densitometry analysis from stem cross sections failed as a means to determine past growth rates. The addition of fertiliser and water increased basal area increment and shoot length. Conflicting results were evident with respect to the role of competition. Nearest-neighbour analysis from a number of sites suggested that competition was not important at most, but not all, sites. Yet, the strong negative relationship between relative growth rate and stand basal area, and growth enhancement from a thinning study, indicated that competition is a significant factor affecting individual tree and stand productivity.

Most of annual production is allocated to leaves, other than in large trees, where the increase in the wood component is the largest contributor to total production. Production of deadwood was consistent from year to year, at approximately 1.7 % of standing biomass. Most litterfall occurs during the first months of winter (April - June), and occurs during a shorter period in toplands than bottomlands. Annual litterfall ranged from 90 - 360 g/m² and was strongly related to stand basal area and biomass. Over 80 % of litterfall was leaves. Fruit production varied between years, both in the amount per tree, and the proportion of trees bearing fruits. In more arid situations and years, only the larger trees bear

fruit. Trees start to bear fruit, given adequate rainfall, at approximately 20 % of their maximum potential size, and all individuals of a given species fruit once larger than two-thirds of their maximum potential size. At 1.5 - 2.0 % of stand biomass, extrapolated fruit production was higher than has been recorded in other studies.

Wood harvesting has a marked impact on woody community structure and biomass and hence productivity. Relative growth rates are increased because of the dominance by smaller, faster growing stems. Absolute yields are reduced because of the lowered basal area and biomass. All species examined demonstrated strong coppicing ability. Within a species, the number of coppice shoots was positively related to cutting height. Between species, the density of coppice shoots per stump was negatively related to the maximum potential height of the species. Pruning of regrowth of *Terminalia sericea* significantly accelerated regrowth of the remaining coppice shoots, although this was interactive with mean shoot number. Turn around times to the next harvest ranged from 3 - 9 years depending on original stem size.

Fire had complex impacts on woody community structure and biomass, and hence productivity. The impact of fire at the scale of an individual tree was dependent upon tree size and fuel load. The smaller the stem and the higher the fuel load, the greater was the proportion of stems killed during a fire. Over 50 % of stems less than 5 cm in circumference were killed during burning. Overall, approximately 6.5 % of stems were killed, and approximately 23 % were unaffected by fire. The rest experienced some degree of damage and resprouted either from the roots, from aerial portions, or both. Overall community structure is significantly altered by fire, and a predictable pattern is evident in relation to fire frequency. The mean biomass, height and circumference decreases with increasing fire frequency, whilst stem density increases. The change to a site dominated by smaller stems with less biomass per unit area results in a higher relative basal area increment, but a lower absolute basal area increment. The effects of fire on germination of woody plant seeds appears to be species specific, with some being stimulated and some being inhibited by fire. Consequently, fire may also facilitate a change in community species composition.

DECLARATION

I declare that this thesis is my own unaided work, except where acknowledged. No part of this thesis has previously been submitted for any degree or examination to any other University.

A handwritten signature in black ink, appearing to read 'Chabala', written in a cursive style.

Klaserie, September 1997

ACKNOWLEDGEMENTS

During the course of a project that spans more than four years many people have an impact, provide assistance, or supply materials. This project is no exception. Over the duration of this project I have become indebted to many people and organisations that have lent moral and material support. These include:

My wife and children who bore the brunt of it all;

The Green Trust, Wits Rural Facility, and Forestek for financial support that made the study possible;

My supervisors Dr Bob Scholes, who stimulated me to keep the project going, and guided me around, through or over any problems that arose, and Prof. Norman Owen-Smith provided the University link and the necessary mental challenges as data became available;

My WRF colleagues, past and present, but especially Prof. John Gear for his understanding and support, Joan Mavrandonis for encouragement and making sense of my poor accounting, and Simon Mdaka and Freddy Mathabela who gave their all so often;

The reserve managers and land owners that made me so welcome on their land, including the Natal Parks Board, the then Tranvaal Provincial Administration, Boputhatswana Parks Board, KaNgwane Parks Board, the Evans', the Rushworth's, the Minaar's, Lydenburg Municipality, Klaserie Private Nature Reserve, Lapalala Wilderness Trust, Ben Lavin Nature Reserve, Klipriviersberg Nature Reserve Association, and Kruger National Park. In particular Phillip Oosthuizen of Hoedspruit Nature Reserve, and Riaan de Lange of Bushbuckridge Nature Reserve deserve special mention, as both allowed me relatively open access to their reserves with little in return;

Jacky Galpin, Marna van der Merwe, Johann Baloyi, Andre Potgieter, and Michele Venter provided specialist assistance for particular sections of the work, without which some would not have been achieved. Peter Scogings kindly collected data from two plots from Fort Hare University farm and made them available to me.

CONTENTS

ABSTRACT	ii
DECLARATION	iv
ACKNOWLEDGMENTS	v

SECTION A: INTRODUCTION

1. GENERAL INTRODUCTION	1
1.1 PRIMARY PRODUCTION IN ECOSYSTEM STUDIES	1
1.2 WOODY PRODUCTIVITY AND SUSTAINABLE LIVELIHOODS	1
1.3 PRODUCTIVITY IN TERRESTRIAL ECOSYSTEMS	2
1.4 PRODUCTIVITY IN SAVANNAS	3
1.4.1 Determinants of savannas	4
1.4.1.1 Soil moisture	4
1.4.1.2 Soil nutrients	5
1.4.1.3 Fire	5
1.4.1.4 Herbivory	6
1.4.1.5 Humans	6
1.4.2 Savanna productivity	7
1.5 DEFINITION OF TERMS	7
1.6 WOODY PRODUCTIVITY	8
1.6.1 Woody versus herbaceous productivity in savannas	8
1.6.2 Components of woody productivity	8
1.6.3 Determinants of woody productivity	9
1.6.4 Issues and uncertainties	10
1.7 OBJECTIVE OF THIS STUDY	11
1.7.1 Objective	11
1.7.2 Goals	11
1.8 APPROACH TO THIS STUDY	11
1.9 STRUCTURE OF THE THESIS	12
2. INTENSIVE STUDY SITES: VEGETATION DESCRIPTION	14
2.1 INTRODUCTION	14
2.2 OBJECTIVES	14
2.3 STUDY AREAS	14
2.3.1 Location	14
2.3.2 Geology and soils	15
2.3.3 Rainfall	16
2.3.4 Vegetation	16
2.3.5 Fauna	17
2.3.6 Land use	17
2.4 METHODS	18

2.5 RESULTS	19
2.5.1 Woody structure	19
2.5.2 Size class distribution	19
2.5.3 Proportion of regenerative stems	19
2.5.4 Species composition	22
2.6 DISCUSSION	22

SECTION B: WOODY PRODUCTIVITY

3. WOODY PLANT GROWTH AND DEATH ACROSS A RANGE OF SITES	26
3.1 INTRODUCTION	26
3.2 OBJECTIVES	27
3.3 METHODS	27
3.4 RESULTS	30
3.4.1 Status of marked stems	30
3.4.2 Absolute growth rates (corrected for death)	31
3.4.3 Absolute growth rates and site variables	32
3.4.4 Relative growth rates (corrected for death)	34
3.4.5 Relative growth rates and site variables	35
3.4.6 Mortality rates	38
3.4.7 Relationship to site variables	41
3.5 DISCUSSION	41
3.5.1 Growth	41
3.5.2 Mortality	50
4. EXTENDING THE TIME FRAME USING DENSITOMETRY	52
4.1 INTRODUCTION	52
4.2 OBJECTIVES	53
4.3 METHODS	53
4.4 RESULTS	55
4.4.1 Species selection	55
4.4.2 Ring width in relation to rainfall	55
4.5 DISCUSSION	57
5. THE INFLUENCE OF WATER AND FERTILISER	60
5.1 INTRODUCTION	60
5.2 OBJECTIVES	60
5.3 METHODS	60
5.4 RESULTS	62
5.4.1 Effects of water and fertiliser	62
5.4.2 Foliar analyses	64
5.5 DISCUSSION	64

6. THE PREVALENCE AND ROLE OF COMPETITION	67
6.1 INTRODUCTION	67
6.2 OBJECTIVES	68
6.3 METHODS	68
6.4 RESULTS	69
6.4.1 Inter-specific competition	69
6.4.2 Intra-specific competition	70
6.5 DISCUSSION	70
7. THE ROLE OF COMMUNITY PHENOLOGY	78
7.1 INTRODUCTION	78
7.2 OBJECTIVES	79
7.3 METHODS	79
7.4 RESULTS	80
7.4.1 Leaf buds/initials	80
7.4.2 Emergent leaves	80
7.4.3 Mature leaves	80
7.4.4 Shoot elongation	84
7.4.5 Buds and flowers	84
7.4.6 Immature fruits	84
7.4.7 Mature fruits	84
7.4.8 Senescent leaves	85
7.4.9 Leafless	85
7.4.10 Fruits from the previous season	86
7.5 DISCUSSION	86
8. SEEDLING RECRUITMENT AND SURVIVAL	89
8.1 INTRODUCTION	89
8.2 OBJECTIVES	90
8.3 METHODS	90
8.4 RESULTS	90
8.5 DISCUSSION	91
SECTION C: PRODUCTION OF HARVESTABLE COMPONENTS	
9. BIOMASS RELATIONSHIPS AND GROWTH RATIOS OF SELECTED SPECIES	96
9.1 INTRODUCTION	96
9.2 OBJECTIVES	96
9.3 METHODS	97
9.4 RESULTS	98
9.4.1 Total mass	98
9.4.2 Dry mass of wood	99
9.4.3 Mass of twigs and leaves	101

9.4.4 Ratio of wood to leaf production	102
9.5 DISCUSSION	104
10. DEADWOOD	107
10.1 INTRODUCTION	107
10.2 OBJECTIVES	107
10.3 METHODS	108
10.4 RESULTS	108
10.5 DISCUSSION	110
11. LITTER	113
11.1 INTRODUCTION	113
11.2 OBJECTIVES	113
11.3 METHODS	114
11.4 RESULTS	115
11.5 DISCUSSION	118
12. FRUIT	121
12.1 INTRODUCTION	121
12.2 OBJECTIVES	121
12.3 METHODS	122
12.4 RESULTS	123
12.4.1 Fruit production profiles	123
12.4.2 Size class of first and maximal fruiting	127
12.4.3 Allometry	127
12.5 DISCUSSION	130
SECTION D: WOOD HARVESTING	
13. A REVIEW OF COMMUNITY LEVEL IMPACTS	133
13.1 INTRODUCTION	133
13.2 IMPACTS ON WOODY COMMUNITY STRUCTURE	134
13.3 IMPACT ON WOODY PRODUCTIVITY AND ASSOCIATED PROCESSES	135
14. PLANT LEVEL IMPACTS: THE INFLUENCE OF STUMP DIMENSIONS AND POST-HARVEST PRUNING ON REGROWTH	138
14.1 INTRODUCTION	138
14.2 OBJECTIVES	139
14.3 METHODS	139
14.3.1 Coppice regrowth of different species	139

14.3.2	Regrowth of <i>T. sericea</i>	140
14.4	RESULTS	142
14.4.1	Coppice regrowth of different species	142
14.4.2	Effects of original stem size on regrowth of <i>T. sericea</i>	144
14.4.3	Effects of cutting height on regrowth of <i>T. sericea</i>	144
14.4.4	Effects of pruning on regrowth of <i>T. sericea</i>	148
14.4.5	Harvester requirements and turnover time	149
14.4.6	Root coppice of <i>T. sericea</i>	150
14.4.7	Browsing of <i>T. sericea</i>	151
14.5	DISCUSSION	152
15.	PLANT LEVEL IMPACTS: EFFECTS OF HARVESTING ON GROWTH OF THE NEIGHBOURING TREE	156
15.1	INTRODUCTION	156
15.2	OBJECTIVES	157
15.3	METHODS	157
15.4	RESULTS	158
15.5	DISCUSSION	158
SECTION E: FIRE		
16.	COMMUNITY LEVEL IMPACTS: INFLUENCE ON WOODY COMMUNITY STRUCTURE	161
16.1	INTRODUCTION	161
16.2	OBJECTIVES	162
16.3	METHODS	163
16.4	RESULTS	164
16.4.1	Biomass	164
16.4.2	Basal area	165
16.4.3	Density	166
16.4.4	Height	166
16.4.5	Number of stems/plant	166
16.4.6	Number of species/transect	167
16.4.7	Proportion of regenerative stems	167
16.4.8	Soils	167
16.5	DISCUSSION	168
17.	PLANT LEVEL IMPACTS: TREE AND SEED MORTALITY AND SURVIVAL	171
17.1	INTRODUCTION	171
17.2	OBJECTIVES	172
17.3	METHODS	172
17.3.1	Mortality of individual stems	172
17.3.2	Seed germination	173
17.4	RESULTS	174

17.4.1 Mortality of individual stems	174
17.4.2 Seed germination	176
17.5 DISCUSSION	178
17.5.1 Mortality of individual stems	178
17.5.2 Seed germination	179

SECTION F: SUMMING UP

18. SUMMARY AND SYNTHESIS	181
18.1 WOODY PRODUCTIVITY	181
18.2 WOODY PRODUCTIVITY AND ENVIRONMENTAL CORRELATES	183
18.2.1 Rainfall	184
18.2.2 Edaphic factors	186
18.2.3 Competition	187
18.2.4 Mortality	188
18.2.5 Stem size	189
18.3 BROAD-LEAVED AND MICROPHYILLOUS SAVANNAS	190
18.4 MANAGEMENT OF WOODY PRODUCTIVITY	191
19. REFERENCES	194

LIST OF FIGURES

Fig 2.1	Location map of intensive study sites	15
Fig 2.2	Size class profiles of woody plants at the arid, semi-arid and mesic localities	21
Fig 2.3	Proportion of regenerative stems at each locality	21
Fig 2.4	Proportion of spinescent and <i>Mimosaceae</i> species at each locality	24
Fig 3.1	Distribution of study localities	28
Fig 3.2	Annual relative change in basal area	36
Fig 3.3	Basal area change relative to stem size (1994/95)	37
Fig 3.4	Stem mortality rate relative to stem size	39
Fig 3.5	Relationship between stem shrinkage and mortality	40
Fig 3.6	Stem mortality and Mean Annual Rainfall	41
Fig 3.7	Mean absolute change in basal area and Mean Annual Rainfall	46
Fig 3.8	Mean relative change in basal area and Mean Annual Rainfall	46
Fig 3.9	Relationship between rainfall and basal area increment at Wits Rural Facility	48
Fig 3.10	Mean absolute change in basal area relative to stand basal area	49
Fig 3.11	Mean relative change in basal area relative to stand basal area	49
Fig 4.1	Example of (a) a good trace and (b) a poor trace	58
Fig 5.1	Influence of water and fertiliser on relative basal area increment	63
Fig 6.1	Canopy height:width ratio for two species with contrasting architecture	73
Fig 6.2	Schematic representation of the problems of nearest neighbour analysis with temporal changes in competitive interactions	74
Fig 6.3	Schematic representation of nearest neighbour analysis and spatial interpretation of competition	76
Fig 7.1	Phenophases at the arid, semi-arid and mesic localities on toplands and bottomlands	81
Fig 8.1	Seedling recruitment and rainfall (1994/95)	92
Fig 8.2	Seedling survival and relative growth rate relative to height size class	92
Fig 9.1	Leaf:twig ratios of mesophyllous and microphyllous species	102

Fig 10.1 Annual deadwood yield relative to stand biomass	110
Fig 11.1 Litterfall at the arid, semi-arid and mesic localities	116
Fig 11.2 Litter yield per standing biomass	117
Fig 12.1 Fruit presence profiles for selected species	124
Fig 12.2 Stem size at which (a) first fruiting, and (b) 100 % fruiting occurs relative to maximum potential stem size	127
Fig 14.1 Number of <i>T. sericea</i> coppice shoots per stump under different treatments	145
Fig 14.2 Mean coppice shoot length of <i>T. sericea</i> per stump under different treatments	146
Fig 14.3 Cumulative length of coppice shoots of <i>T. sericea</i> per stump under different treatments	147
Fig 14.4 The proportion of root coppice shoots	151
Fig 14.5 Browsing frequency	152
Fig 15.1 Relative basal area increment relative to newly available resource space	159
Fig 16.1 Proportion of regenerative stems across a range of fire frequencies	168
Fig 17.1 Woody stem mortality relative to fire fuel load	175
Fig 17.2 Fate of woody stems after burning	176

LIST OF TABLES

Table 1.1 Summary estimates of net primary production per major world biome	3
Table 2.1 Woody community structural characteristics at the arid, semi-arid and mesic localities	20
Table 2.2 Species contributing 2 % or more to the density, biomass or basal area at each locality	23
Table 3.1 Status of marked stems after each year	31
Table 3.2 Net change in stand basal area on annual basis	32
Table 3.3 Forward stepwise regression results of absolute change in basal area against 25 site variables	33
Table 3.4 Forward stepwise regression results of absolute change in basal area for clay and sandy sites	34
Table 3.5 Forward stepwise regression results of relative change in basal area against 25 site variables	38
Table 3.6 The proportion of stems that shrunk during year _(t) that died during the following year _(t+1)	40
Table 4.1 Species tested via densitometry analysis	56
Table 5.1 ANOVA table for relative change in basal area for first growing season	62
Table 6.1 Comparison of site attributes for sites with and without interspecific competition	69
Table 6.2 Comparison of site attributes for sites with and without intraspecific competition	70
Table 7.1 Proportion of evergreen and deciduous stems with mature leaves during winter at the arid site	85
Table 8.1 Survival, mortality and recruitment of seedlings in permanent quadrats at 22 localities throughout the savanna biome	91
Table 9.1 Regression relationships per species between log(dry mass) and stem circumference	98
Table 9.2 Dry mass as a percentage of fresh mass	99
Table 9.3 Regression relationships between wood mass components and stem circumference	100

Table 9.4 Regression relationships between mass of leaves, mass of twigs and stem circumference	101
Table 9.5 Regression of mean relative change in basal area per stem circumference	103
Table 9.6 Leaf production as a proportion of total aboveground production per stem	103
Table 10.1 Annual harvestable dead wood yield from the arid, semi-arid and mesic localities	109
Table 11.1 Proportion of annual litterfall during the four months with the highest input	115
Table 11.2 Composition of the litterfall	119
Table 12.1 Summary relationships between fruit dry mass per species per year and tree dimension	128
Table 12.2 Relationship between fruit production and transect basal area and biomass	129
Table 12.3 Estimated total fruit production for all species	130
Table 14.1 Relationship between number of coppice shoots per cut stump and independent variables	142
Table 14.2 Mean unit area per coppice shoot per species	143
Table 14.3 Dimensions of <i>T. sericea</i> logs in fuelwood bundles cut by local harvesters	149
Table 14.4 The influence of cutting height, stems size and pruning on the harvest interval	150
Table 16.1 Attributes of woody community structure relative to fire frequency	165
Table 17.1 Characteristics of each experimental burn	172
Table 17.2 Fate of marked stems after eight experimental burns	175
Table 17.3 Influence of burning on percentage seed germination of surface and buried seeds	177
Table 18.1. Mean production per tree component per year	183

GENERAL INTRODUCTION

1.1 PRIMARY PRODUCTION IN ECOSYSTEM STUDIES

Productivity has been a unifying theme across theoretical and applied research for several decades. To the theorist, understanding productivity provides insights into carbon and energy flows and ecological efficiencies in the food chain (Pomeroy & Service 1986). It represents an integration of several biological and ecological processes. To the applied researcher and manager, productivity symbolises the end product of one's labours and interventions; something that can be manipulated and improved towards a higher economic gain. As such, it is one of the few areas of ecological research than can be truly interdisciplinary with disciplines within and outside the biological realm.

In the last two decades or so, productivity of natural and man-made systems has attained an even greater significance in the face of an increasing world population and the accumulation of greenhouse gases in the atmosphere. The first demands greater productivity to meet human demands. This may be through intensification of man-made systems, but also increased harvesting from and management of extensive natural systems. There is little room for economically unproductive tracts of land in a food- and job-hungry world. The second means that carbon dynamics and storage are of major interest and concern. More precise estimates of natural primary productivity are required to provide the detailed regional budgets of carbon gains and losses, as well as mechanisms to improve primary productivity and thereby immobilise some of the build up of carbon dioxide in the atmosphere (Eamus & Jarvis 1989, Solbrig *et al.* 1991, Myneni & Los 1995, Scholes & Hall 1996). Slowing of the rates of deforestation is regarded as a major element in a suite of strategies to combat global warming (O'Brien 1996).

1.2 WOODY PRODUCTIVITY & SUSTAINABLE RURAL LIVELIHOODS

It is implicit in the search for reliable determinations of woody productivity that these values will be used in appropriate management and policy fora, i.e. the knowledge will be used to make more informed and hence improved decisions. At an applied level, the value of woody productivity is particularly pertinent in

southern Africa in the realm of rural community development and natural resource management systems. Both have explicit links to nature conservation and cattle ranching.

Rural communities use a variety of products harvested from lands around their homestead or settlement. Trees are a major contributor, having multiple uses, including fuelwood, construction timber, carving timber, medicines, fruits, browse and dyes. Trees may also provide the necessary habitat or food for other harvested resources, such as woodroses and mopane worms. The direct multiple use value of trees is not equalled by any other life form. The indirect benefits are of equal importance.

In South Africa many rural communities face a shortage of these resources because of high human population densities in the rural areas, largely a result of translocations during the apartheid era (Grossman & Gandar 1989). This has frequently broken traditional management systems and traditions that governed the harvesting of resources and maintenance of the resource base. Hence a recent focus emerging during the last few years on the value of trees and appropriate management systems to maintain tree biomass and maximise potential benefits from trees. Several conservation agencies also base their neighbour relations programmes with adjacent rural communities on the supply of resources, such as wood and fruits (e.g. Hughes 1994). All these users are interested in the value of products from woody plants, and sustainable harvesting levels and mechanisms. Entrepreneurial opportunities from sustainable harvesting of such products commercially are viewed as one means of providing much needed income opportunities (Shackleton 1996), scaling up the already prevalent trade in woody resources (Gandar 1994a, Dzerefos *et al.* 1995). Despite this interest in products from woody plants, the predictive knowledge-base required for the long-term management and enhancement of woody resources is lacking.

1.3 PRODUCTIVITY OF TERRESTRIAL ECOSYSTEMS

There is a wide range in primary productivity from one ecosystem to the next (Table 1.1), as well as within ecosystems. The open oceans contribute a considerable proportion of total global production by virtue of covering 70 % of the globe. However, on a per unit area basis, they are surpassed by terrestrial ecosystems that include a woody component. Tropical forests are widely regarded as the most productive ecosystems, followed by temperate forests and then savannas.

Table 1.1. Summary estimates of net primary production per major world ecosystem.

ECOSYSTEM	ANNUAL NET PRIMARY PRODUCTION (g/m ² /yr)			
	Whittaker (1975)	McNaughton & Wolf (1979)	Ajtay <i>et al.</i> (1979)	Melillo <i>et al.</i> (1993) ¹
Forests - tropical	2 000	2 000	2 200	2 270
Forests - temperate	1 250	1 300	1 250	1 430
Savannas	900	700	900	850
Grasslands	600	300	600	630
Desert	40	70	90	120
Tundra	140	200	140	260
Fresh water	250	200	400	
Marine - pelagic	125	125	125	
Marine - coastal	360	350	360	
Marine - estuarine	1 800	2 000	1 500	

¹Converted from g C to g Organic mass = x 2.3

1.4 PRODUCTIVITY IN SAVANNAS

Savannas are one of the world's major terrestrial ecosystems, comprising between 10 % and 15 % of the world's land surface, depending upon definition. Distributed across nearly all the continents, they occur in broad bands between the equatorial forests and mid-latitude deserts. Approximately 50 % of the African continent, and one third of South Africa are savannas. They are home to over 30 % of the world's population (Solbrig *et al.* 1991). The majority of the world's savannas, including South Africa, are managed as extensive ranching areas (Grossman & Gandar 1989).

Savannas are an unusual vegetation formation because of the codominance of herbaceous and woody components. Whilst each component has both positive and negative feedbacks on the other, it can be hypothesised that the presence of two well developed components could result in a higher combined

productivity per unit area for the system as a whole relative to other ecosystems. This does not appear to be the case (Whittaker 1975, McNaughton & Wolf 1979), and is a reflection of the particular suite of determinants that characterise savanna structure and function, and hence productivity. Nevertheless, it is now appreciated that savannas are considerably more productive than once believed (Scholes & Hall 1996).

1.4.1 Determinants of savannas

It is generally argued that savanna structure and function is broadly determined by the interplay of four major determinants: soil moisture, soil nutrients, fire and herbivory (Frost *et al.* 1986, Skarpe 1992, Teague & Smit 1992, Scholes & Walker 1993). The first two are frequently termed the primary determinants since they affect the potential structure and function in the absence of the other two, usually referred to as secondary determinants. Humans are also being recognised as an equally important secondary determinant. Recently Jeltsch *et al.* (1996) concluded that these determinants alone were insufficient to explain the coexistence of a woody and herbaceous component and hence savanna structure and function of an modelled arid savanna. Several other minor determinants are recognised for specific localities but are not considered important at the biome scale, for example temperature (Teague & Walker 1988). The effects of the determinants are interactive.

1.4.1.1 Soil moisture

The key aspects of climate are temperature and the seasonality of precipitation. Together they are the overriding determinants of plant available soil moisture, along with the smaller scale determinants of soil texture and aspect.

The higher the duration of adequate soil moisture the greater will be the biomass of vegetation, woody and herbaceous, except in waterlogged soils. Generally arid savannas occur in areas where the mean annual rainfall averages from 250 mm to \pm 800 mm, intergrading into moist savannas which occur between \pm 700 mm and 1 800 mm.

Soil texture modifies the availability of precipitation received. Infiltration and hydraulic conductivity are

higher in sandy soils than clay soils. Clay soils have a higher water holding capacity but at lower conductivities. Consequently, in low to medium rainfall areas, sandy soils offer greater plant available water, and are thus characterised by a higher plant biomass than on clay soils under similar rainfall. At higher rainfall, the opposite occurs because the saturation of clays negates the effects of the low conductivity. Additionally, at high rainfalls, sands are prone to greater leaching than clays. The effects of soil texture are interactive with the effects of soil nutrients because of the higher nutrient status of clays. Scholes (1990a) has argued that available moisture determines the duration of the growing period, but soil nutrients control the growth rate.

Slope aspect affects soil moisture through its effect on incoming radiation flux and hence evaporation, as well as the gravitational effects on the movement of soil moisture and soluble nutrients.

1.4.1.2 Soil nutrients

Higher soil nutrient status generally leads to higher plant productivity, and this holds true for savannas. In savannas this simple relationship is modified by the effects of rainfall and plant available moisture. High rainfall promotes leaching, which in turn is slowed by the soil exchange capacity depending upon soil texture and clay type. Low rainfall results in low leaching, but also low plant available moisture. Because plants take up nutrients in solution, if plant available moisture is low even highly eutrophic soils will have a low productivity. This is particularly pertinent with respect to the availability of soil nitrogen.

1.4.1.3 Fire

Fire's major effect on savanna structure and productivity is through its impact on plant recruitment and mortality (especially the smaller size classes). The effect of fire interacts with the primary determinants in that there has to be sufficient fuel load for fire to occur. Thus, arid savannas only experience high intensity fires relatively infrequently because of the time required to accumulate sufficient burnable material. In areas conducive to regular fires, savanna biomass and stature is lowered by frequent burning because woody plant recruitment is constrained. This may promote productivity on a individual plant basis because of reduced competition and the higher productivity of smaller stems, but overall area-based productivity

diminishes. This may be compensated for by increased belowground biomass and productivity but requires further study. The role of changes in soil nutrient status under frequent fires, and how that affects woody production also requires further study.

1.4.1.4 Herbivory

Herbivory effects the absolute amounts of plant material, as well as the tree to grass ratio. It is usually spatially and temporally variable, enhancing patchiness in the environment. Rapid increases in woody density have been attributed to excessive grazing of the herbaceous layer. Heavy browsing does not appear to stimulate a similar reaction in the herbaceous layer. Browsing affects the recruitment of woody plants, and hence community density and structure. Herbivores favour eutrophic savannas or eutrophic patches within dystrophic savannas, despite higher productivities. This may result in a lower plant biomass in eutrophic savannas relative to dystrophic ones under the same rainfall. There is some suggestion that concentrations of herbivore activity may sustain such eutrophic patches (Blackmore, *et al.* 1990). Herbivory accelerates nutrient cycling. The timing of herbivory relative to other environmental stress, such as drought or post-fire period may have long-term effects on community composition, structure and productivity.

1.4.1.5 Humans

Humans have impacted on savanna structure and hence potential productivity for millennia. Impacts vary in scale, frequency, intensity, duration and persistence. The degree of persistence is particularly pertinent as in many instances the effects of human activities alter the local abiotic environment so that savanna structure and function are permanently altered, even after the end to direct human activities in the area. For example, the conversion of broadleaved dystrophic savannas to self-sustaining eutrophic microphyllous savanna on sites of Iron Age occupation (Blackmore, *et al.* 1990, Scholes & Walker 1993), or the enhanced recruitment of *Acacia tortilis* at abandoned kraal sites of Turkana pastoralists (Reid & Ellis 1995). The long historical role of humans in modifying vegetation structure and productivity is not confined to savannas (e.g. Denevan 1992). In modern times humans have had an accelerated impact on savanna structure over large tracts through clearance, selective thinning, and harvesting of a range of products, as well as manipulation of the fire regime and levels of herbivory (Grossman & Gandar 1989).

The interaction of these determinants, coupled with the inevitable local exceptions, results in a wide variety of different savanna types, ranging from open grasslands with few trees, through to dense, tall woodlands with a continuous canopy, but still with an established herbaceous layer. Woody basal area in savannas ranges from less than 0.5 m²/ha to 32 m²/ha (Shackleton 1994a); a 60 fold difference. Savannas transitional to forest may have basal areas of up to 33 m²/ha (Chidumayo 1993).

1.4.2 Savanna productivity

Because of the wide range in savanna types and ratios of woody to herbaceous standing crop and the interplay of each component on the other, it is hardly surprising to find a considerable range in savanna productivity. Annual herbaceous productivity alone ranges from less than 100 kg/ha to over 2 500 kg/ha (Rutherford 1978). Regression equations derived by Scholes and Hall (1996) provide a range in total annual production of less 200 g/m² to over 3 000 g/m² with most falling within the range of 1 200 - 1 400 g/m². However, the number of empirical studies relative to the global expanse of savannas is inadequate to capture the true range of total productivity.

1.5 DEFINITION OF TERMS

- a. *Savanna* refers to a neotropical vegetation type in which fire-adapted, co-dominant herbaceous and tree strata experience markedly seasonal growth patterns in relation to the seasonal delivery of precipitation. In Africa, several classifications exist subdividing the biome on the basis of water availability (Huntley 1982, Rutherford & Westfall 1986), soil nutrient status (Huntley 1982, Scholes 1990a), structure (Cole 1986) and floristics (e.g. White 1980, Acocks 1988).
- b. *Primary production* is the mass of living plant material produced per unit time (Dajoz 1977) as a result of the conversion of radiant energy into chemical energy through the process of photosynthesis. In this project only aboveground production is considered.
- c. *Woody plant* is a collective term to include both trees and shrubs. It is synonymous with phanerophyte according to Raunkier's (1934) terminology.

1.6 WOODY PRODUCTIVITY

Total above ground woody productivity is still a relatively unknown value in southern African and world savannas. Some components, such as stem increment or browse production, have been measured, but not all components from the same stand at the same time. The best available estimate from Scholes & Walker (1993) of 2.8 t/ha/yr was derived from a series of disparate studies in the same area. The range in woody productivity across contrasting rainfall regimes and soil types is unknown. Even at the level of individual trees a recent review commented that there is only limited information regarding the growth rate of savanna trees (Smit *et al.* 1996).

1.6.1 Woody versus herbaceous productivity in savannas

Parallelling the range in savanna types is the probable range in productivity, and its division between the herbaceous and woody components. Scholes & Walker (1993) found a relatively equitable division of total productivity between the herbaceous and woody components. Woody plants accounted for $\pm 64\%$ of the total aboveground productivity (best estimates). Menaut & Cesar (1982) studying four savanna facies along a continuum of increasing woody density (up to 1 500 trees/ha) in Ivory Coast, reported that woody productivity contributed only 1,7 % to 20,1 % of the total productivity, corresponding to 3,6 % to 30,3 % of total aboveground productivity. Ovington (1963) found that 64 % of total aboveground production in a temperate oak savanna was from woody plants. Kelly & Walker (1976) found that browse production alone was greater than herbaceous production at five sites in Zimbabwe. At four other sites browse constituted between 25 % and 44 % of aboveground productivity where only herbaceous and browse production were measured. Thus, it is apparent that although there is a wide range in the ratio of woody to herbaceous productivity, that woody plants can contribute up to two-thirds of aboveground production in savannas, through to almost 100 % grading into woodlands and forests.

1.6.2 Components of woody productivity

Woody productivity can be divided into a series of components corresponding to the productivity of the different organs of a woody plant. A major division is between aboveground plant parts and belowground

parts, namely the roots. Few studies have quantified both aboveground and belowground woody productivity from the same site during the same season. Belowground productivity has been estimated using the ratio of aboveground to belowground standing crop and assuming the same ratio for above- to belowground productivity. Yet, it is readily accepted that production rates of the different aboveground components (wood, bark, shoots, leaves, fruits) are not equal, therefore it is erroneous to assume that productivity rates applicable for the total above ground biomass are the same for the total belowground biomass. Estimates from the Nylsvley savanna indicates that approximately 40 % of total woody productivity is below ground (Scholes & Walker 1993). Slightly lower values were measured in several temperate forest sites (Nadelhoffer *et al.* 1985), although values up to 65 - 70 % has been suggested (Raich & Nadelhoffer 1989, Scholes & Hall 1996). Substantial progress is required before sufficient, accurate measurements are available, from which summary conclusions and generalities can be made.

Of the aboveground organs, total productivity is the sum of the productivity of wood, twigs, leaves, flowers and fruits. Leaves and twigs are frequently considered together as browse. Production of flowers and fruits are rarely measured.

Given the applied nature of this study I find it useful to categorise woody productivity according to utilisable components rather than plant organs, although there is overlap. Consequently, the major components (generalist use) are livewood, deadwood, browse and fruits. Minor components (specialist use) are bark, roots and sap (especially for dyes). This study concentrated on the major utilisable components.

1.6.3 Determinants of woody productivity

On a continental and landscape level the distribution, structure and function of savannas have been correlated with climatic and soil characteristics (see Sect. 1.4). It is therefore implicit that these two factors also determine the gross productivity of savannas, modified by fire, herbivory and man.

At the level of an individual plant, woody productivity is determined by the balance between photosynthesis and respiration. The external variables determining the rate of one or both of these two processes include radiant flux density light intensity, concentration of atmospheric carbon dioxide, air temperature and water availability (Lambers & Poorter 1992).

Between these two scales is woody community or stand level productivity, and its determinants. Extrapolation from plant level studies is problematic because of the influences neighbouring plants have upon one another through shading and competition, thereby altering the values of the controlling variables, and subsequent rates of net photosynthesis. Interpolation from the landscape level is not possible, as productivity *per se* has not been widely measured at that level, simply the distribution and structure of savannas. With notable exceptions, estimates derived from satellite-based techniques frequently suffer from inadequate ground-truthing (Kgathi *et al.* 1994).

At the stand level, estimates of woody productivity have been made for several savannas (e.g. Kelly & Walker 1976, Rutherford 1978, Scholes & Walker 1993). These have provided a range of productivity estimates mirroring the diversity of savanna types. Very few studies provide estimates from more than two sites over more than one or two growing seasons, and as such can provide only limited insight into why productivity rates differ from one place to another. Few efforts have been made to integrate and compare these findings with one another to generate hypothesis regarding woody productivity. Individual studies have found correlation between woody productivity, or a specific component of woody productivity (such as browse) and current seasons rainfall (Kelly & Walker 1976, Scholes 1990b), previous seasons rainfall (Rutherford & Panagos 1982) and soil nutrient status (Prins & van der Jeugd 1992). These need to be tested in a rigorous fashion, along with structural attributes of the woody community under investigation, such as density, basal area, and size class profile.

1.6.4 Issues and uncertainties

The above overview of savanna woody productivity has highlighted some of the major issues and uncertainties in woody productivity research. These are summarised as key questions below.

- a. What is the range in woody productivity across a range of environments?
- b. What are the key biotic and abiotic determinants of woody productivity at a community level?
- c. What are the respective roles of current seasons and previous seasons rainfall in current season woody productivity?
- d. What is the relationship between stand structure and woody productivity?
- e. What is the range in productivity across the different woody plant components?

- f. What is the impact of management actions on total woody plant productivity and the productivity of utilisable components?
- g. What is the range in belowground woody plant productivity, and its relationship to aboveground woody productivity and site variables?

1.7 OBJECTIVES OF THIS STUDY

1.7.1 Objective

The objective of this study was to gain a predictive knowledge-base of aboveground woody production within the South Africa savanna biome.

1.7.2 Goals

1. To determine aboveground woody plant productivity across a range of environments within the South African savanna biome.
2. To seek relationships between woody productivity and structural and site characteristics.
3. To determine the productivity of the different components of aboveground woody biomass.
4. To explore the effects of management practices on woody plant productivity.

Specific goals are presented in each chapter (Sect. 1.9).

1.8 APPROACH TO THIS STUDY

With the current lack of productivity estimates, gross estimates across the range of savanna types were considered more important than more precise estimates from a few sites. Therefore, the approach was to seek out the inherent variation of savanna structure, rather than select 'representative' sites. This approach facilitates comparison between different savanna types, across the entire range, thereby allowing synthesis

of the data into meaningful relationships to enhance predictive capacity. It also allows model testing and definition of new avenues for investigation.

Predictive capacity can be established at a variety of scales, through employment of different tools, and reporting of a certain suite of statistics. Reflecting my personal preference and strengths, the approach in this study was largely empirical at the level of a woody community. This is also the scale at which management actions are formulated and implemented. Predictive capacity was founded on the derivation of statistical relationships across a range of savanna communities. Scope exists for this to be integrated at a higher level into basic mechanistic models, but was not pursued here.

Although one of the primary goals was to identify the determinants of woody productivity through comparison of production from a range of habitats, it was implicit throughout the design of the study, on the strength of previous work, that water availability was a major factor. Consequently, most components of the study were replicated across a rainfall gradient.

1.9 STRUCTURE OF THE THESIS

This thesis has been divided into six sections (A - F). Each section groups a few chapters around a common theme:

SECTION A: Introduction

- Chap. 1. General introduction
- Chap. 2. Intensive study sites: vegetation description

SECTION B: The range in woody plant productivity

- Chap. 3. Woody plant growth and death across a range of sites
- Chap. 4. Extending the time frame using densitometry
- Chap. 5. The influence of water and fertiliser
- Chap. 6. The prevalence and role of competition
- Chap. 7. The role of community phenology
- Chap. 8. Seedling recruitment and survival

SECTION C: Production of harvestable components

- Chap. 9. Biomass relationships and growth ratios of selected species
- Chap. 10. Deadwood
- Chap. 11. Litter
- Chap. 12. Fruit

SECTION D: Impacts of wood harvesting on woody plant productivity

- Chap. 13. Community level impacts: a review
- Chap. 14. Plant level impacts: the influence of stump dimensions and post-harvest pruning on regrowth
- Chap. 15. Plant level impacts: effects on growth rate of the neighbouring tree

SECTION E: Impacts of fire on woody plant productivity

- Chap. 16. Community level impacts: influence on woody community structure
- Chap. 17. Plant level impacts: tree and seed mortality and survival

SECTION F: Summing up

- Chap. 18. Summary and synthesis
- Chap. 19. References

Section A sets the scene for the reader, and provides the necessary background information. Section B is orientated at addressing the first goal (Sect. 1.7.2), but also contributes to Goal 2. The third goal is largely addressed by Section C, although part of Section B is relevant. The last goal is covered by Sections D and E that deal with wood harvesting, and fire, respectively. Each chapter within sections is presented in a stand-alone format, with a brief introduction of the issue, and more detailed key questions and hypotheses than presented in this Introductory chapter, followed by results and discussion. Chapters are cross-referenced as necessary with Chapter 18 summarising and integrating all components of the study.

INTENSIVE STUDY SITES: VEGETATION DESCRIPTION

2.1 INTRODUCTION

The first two goals of this study (Sect. 1.7.2) necessitated the selection of a series of sites across a range of environments throughout the savanna biome, and the measurement of some component of woody productivity by which to compare the sites. Achievement of the second two goals required more detailed approaches with more frequent measurements. This was only possible at a smaller number of localities. This chapter provides the reader with a description of these more intensive localities. A varying number of plots or transects were sampled at each of the localities according to the requirements for the different sections of the project.

Given that the availability of water for plant growth processes is regarded as the primary determinant of savanna structure and function (Frost *et al.* 1986, Scholes & Walker 1993), it was deemed necessary to replicate all experimental aspects of this project (as far as possible) within contrasting rainfall zones. Consequently three localities were selected along a rainfall gradient for a variety of experimental procedures. For convenience the three localities are referred to as arid (Hoedspruit Nature Reserve), semi-arid (Wits Rural Facility) and mesic (Bushbuckridge Nature Reserve) reflecting their relative positions along the rainfall gradient.

2.2 OBJECTIVE

The objective of this part of the study was to characterise the species composition and structure of the woody vegetation at each of the three intensive monitoring localities.

2.3 STUDY AREAS

2.3.1 Location

All three localities were located in the central lowveld straddling the boundary between Mpumalanga and Northern Province (Fig 2.1). The north-south distance between the localities is approximately