

SOIL, VEGETATION AND LARGE HERBIVORE RELATIONS
IN MKUZI GAME RESERVE, NATAL

Peter Styan Goodman

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.

April 1990

ABSTRACT

The maintenance of biotic diversity is a central aim of conservationists. The purpose of this thesis was to evaluate some hypotheses relating to diversity and to determine the nature of the diversity/biomass relations between the vegetation and large herbivores of Mkuzi Game Reserve.

The interrelations between geology, soils and vegetation were sought using a suite of classification and ordination procedures, and correlation analysis. Soils were strongly associated with underlying geology and topography, and varied from base rich clays to base poor sands and shallow rocky soils at the extremes. Vegetation physiognomy and composition were strongly associated with soils. Woody biomass increased with an increase in available moisture, but had a bimodal response to available nutrients. Soils influenced grass and forb distribution and biomass, as did interactions with woody plants and the effects of utilization and fire.

Beta-diversity was high relative to other southern African savannas, as a result of the high spatial heterogeneity of the landscape. By contrast, high beta-diversity at the community scale was associated with a benign environment and low disturbance.

Woody species richness was positively related to productivity. Grass species richness was positively related to productivity and utilization, but negatively influenced by woody biomass. Forb species richness was determined by interactions with woody plants, grasses and the intensity of utilization.

The herbivore community was below carrying capacity and dominated by concentrate feeders. This was a result of disturbance rather than any biological characteristic of the system. Herbivore biomass was positively related to vegetation biomass when this was limiting, thereby supporting the notion that productivity of herbivores is directly related to resource supply rate.

The richness of herbivores in Mkuzi is a result of the diversity of habitats. However, the local richness and diversity of herbivores

was negatively related to spatial heterogeneity: this was unexplained and requires further investigation.

Herbivore richness was positively, and equitability negatively related to the local vegetation biomass, richness, diversity and equitability, and herbivore biomass. The former relation supports current theory. The latter is possible in a situation where a generalist species is able to successfully exploit a greater amount and variety of resources.

There is no single determinant of vegetation and herbivore biomass and diversity. They are a function of a complex set of interactions between themselves, the amount and variety of resources, and disturbance.

DECLARATION

I declare that this thesis is my own, unaided work, unless otherwise acknowledged. 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 other University.

P.S. Mphahlele

(Name of candidate)

10 day of April, 1970.

DEDICATION

This work is dedicated to
Cathie, Sally-Anne and Kristi,
for whom writing a thesis has
become part of their way of life.

PREFACE

This research was undertaken whilst in the employ of the Natal Parks Board as Regional Scientist for Mkuzi and surrounding reserves. I thank my employers for the opportunity to undertake this work and for logistic and material support for the duration of the study.

I am indebted to my supervisor Dr Brian Walker who has patiently stimulated, encouraged and advised me throughout the duration of the study. His knowledge of and enthusiasm for ecology and its application has had a profound effect on my education and approach to this and other ecological work I have undertaken.

Mr Jeremia Gumbi has been an invaluable assistant and companion throughout the study. His knowledge of plants and animals, and ability to organise have made a positive contribution to its outcome.

I thank Drs Roy Mottram and Martin Farina of the Soils and Irrigation Research Institute, Cedara for invaluable advice and assistance with the analysis of soil samples. Profs. O.M. Hilliard and K.D. Gordon - Gray of the Bews Herbarium, University of Natal, gave many hours of valuable assistance naming sometimes rather tatty plant specimens. Mike Lambert and Spud Ludbrook gave valuable assistance with field data collection and sample analysis and Tom Smith and Jane Henry (nee Owen) assisted with data processing and statistical analysis. Wendy Bell proof read the text and pointed out many grammatical errors while Fonda Lewis checked the references. Any errors that remain are my own.

Dr Richard Cowling kindly provided facilities for a month in the Botany Department at the University of Cape Town for completing the write-up. He also read some early drafts and pointed out some logical flaws in my arguments and stimulated some interesting discussion.

Finally, Cathie Goodman fought and conquered an inferior computer, two bug ridden word processing packages and expensive but below standard drafting equipment, to turn my near illegible scratchings into what it is now. To her and all others who assisted me in this study, I am most grateful.

PREFACE

This research was undertaken whilst in the employ of the Natal Parks Board as Regional Scientist for Mkuzi and surrounding reserves. I thank my employers for the opportunity to undertake this work and for logistic and material support for the duration of the study.

I am indebted to my supervisor Dr Brian Walker who has patiently stimulated, encouraged and advised me throughout the duration of the study. His knowledge of and enthusiasm for ecology and its application has had a profound effect on my education and approach to this and other ecological work I have undertaken.

Mr Jeremia Gumbi has been an invaluable assistant and companion throughout the study. His knowledge of plants and animals, and ability to organise have made a positive contribution to its outcome.

I thank Drs Roy Mottram and Martin Farina of the Soils and Irrigation Research Institute, Cedara for invaluable advice and assistance with the analysis of soil samples. Profs. O.M. Hilliard and K.D. Gordon - Gray of the Bews Herbarium, University of Natal, gave many hours of valuable assistance naming sometimes rather tatty plant specimens. Mike Lambert and Spud Ludbrook gave valuable assistance with field data collection and sample analysis and Tom Smith and Jane Henry (nee Owen) assisted with data processing and statistical analysis. Wendy Bell proof read the text and pointed out many grammatical errors while Fonda Lewis checked the references. Any errors that remain are my own.

Dr Richard Cowling kindly provided facilities for a month in the Botany Department at the University of Cape Town for completing the write-up. He also read some early drafts and pointed out some logical flaws in my arguments and stimulated some interesting discussion.

Finally, Cathie Goodman fought and conquered an inferior computer, two bug ridden word processing packages and expensive but below standard drafting equipment, to turn my near illegible scratchings into what it is now. To her and all others who assisted me in this study, I am most grateful.

TABLE OF CONTENTS

	Page
ABSTRACT.....	i
DECLARATION.....	iii
DEDICATION.....	iv
PREFACE.....	v
LIST OF TABLES.....	xi
LIST OF FIGURES.....	xiv
1. INTRODUCTION	
1.1 Background and general objectives.....	1
1.2 Approach.....	2
2. STUDY AREA AND DESCRIPTION	
2.1 LOCATION AND SIZE.....	3
2.2 CLIMATE.....	3
2.3 TOPOGRAPHY, GEOLOGY AND GEOMORPHOLOGY.....	9
2.4 SOIL.....	15
2.5 SURFACE HYDROLOGY.....	17
2.6 VEGETATION AND FAUNA.....	18
2.7 PALEOECOLOGY PAST HISTORY AND LANDUSE.....	21
3. LAND TYPES, SOILS AND VEGETATION	
3.1 OBJECTIVES.....	26
3.2 GENERAL APPROACH.....	26
3.3 METHODS.....	30
3.3.1 Sample strategy and field procedure.....	30
3.3.1.1 Environmental information.....	31
3.3.1.2 Geology and soils.....	31

3.3.1.3 Vegetation.....	32
3.3.2 Laboratory analysis and data preparation.....	32
3.3.2.1 Environmental information.....	32
3.3.2.2 Soils.....	33
3.3.2.3 Vegetation.....	35
3.3.3 Data analysis.....	35
3.3.3.1 Multivariate techniques.....	35
3.3.3.2 Data transformation and editing.....	43
3.4 RESULTS.....	44
3.4.1 Soils and land types.....	44
3.4.1.1 Soil ordination and classification.....	44
3.4.1.2 Land type/soil relations.....	50
3.4.2 Vegetation ordination and classification.....	54
3.4.2.1 Determination of sample plot size.....	54
3.4.2.2 Physiognomic classification.....	57
3.4.2.3 Floristic ordination and classification.....	60
3.4.2.3.1 Preliminary analysis of woody vegetation.....	60
3.4.2.3.2 Woody plant ordination and environmental interpretation.....	61
3.4.2.3.3 Herbaceous layer ordination and environmental interpretation.....	70
3.4.2.3.4 Vegetation classification and environmental characterization of groups.....	75
3.5 DISCUSSION.....	81
3.5.1 Methods.....	81
3.5.1.1 Approach, sample strategy and data collection.....	81
3.5.1.2 Analytical techniques.....	82
3.5.2 Results.....	83
3.5.2.1 Soil ordination and classification.....	83
3.5.2.2 Vegetation ordination and classification.....	84
3.5.3 Vegetation stability and dynamics.....	85
4. LARGE HERBIVORE COMMUNITY STRUCTURE AND DYNAMICS	
4.1 INTRODUCTION.....	94
4.2 METHODS.....	94
4.2.1 Population estimation.....	94

4.2.2	Stocking density estimation.....	94
4.2.3	Graze to browse ratio.....	96
4.3	RESULTS	
4.3.1	Density estimates.....	98
4.3.2	Biomass density and relative energy consumption.....	98
4.3.3	Graze to browse ratio.....	104
4.3.4	Historical perspective and recent population dynamics..	104
4.4	DISCUSSION.....	112
5.	A REVIEW AND DISCUSSION OF HYPOTHESES REGARDING DIVERSITY IN ECOLOGICAL COMMUNITIES	
5.1	INTRODUCTION.....	118
5.2	WHAT IS ECOLOGICAL DIVERSITY?.....	118
5.3	SOME HYPOTHESES REGARDING ECOLOGICAL DIVERSITY.....	120
5.4	THE MEASUREMENT OF DIVERSITY.....	128
6.	VEGETATION AND HERBIVORE BIOMASS	
6.1	INTRODUCTION.....	131
6.2	METHODS.....	131
6.2.1	Site selection and measuring period.....	131
6.2.2	Estimation of plant species composition, biomass and structure.....	132
6.2.2.1	Herbaceous plants.....	132
6.2.2.2	Woody plants.....	133
6.2.3	Estimation of large herbivore species composition and biomass.....	137
6.3	RESULTS.....	138
6.3.1	Vegetation biomass and structure.....	138
6.3.1.1	Herbaceous standing crop and biomass.....	138
6.3.1.2	Woody plant biomass.....	138
6.3.1.3	Soil and vegetation biomass relations.....	141
6.3.1.4	Vertical distribution of plant biomass.....	146
6.3.1.5	Woody plant size distribution and dynamics.....	152
6.3.1.6	Species relative abundance distributions.....	156
6.3.2	Large herbivore biomass and relative abundance.....	158

6.4	SUMMARY.....	164
7.	RELATIONS BETWEEN SOIL, VEGETATION BIOMASS AND VEGETATION DIVERSITY	
7.1	INTRODUCTION.....	166
7.2	PLANT SPECIES TURNOVER RATES.....	166
7.3	PLANT SPECIES RICHNESS, RESOURCE GRADIENTS AND DISTURBANCE.....	172
7.3.1	Species richness and soil gradients.....	172
7.3.2	Species richness and plant performance.....	181
7.4	DISTURBANCE AND DIVERSITY.....	185
7.4.1	Utilization and diversity of herbaceous vegetation.....	186
7.4.2	Fire frequency and diversity of herbaceous vegetation..	190
7.4.3	Fire frequency and diversity of woody vegetation.....	193
7.5	SUMMARY.....	193
8.	DIVERSITY AND BIOMASS RELATIONS BETWEEN VEGETATION AND LARGE HERBIVORES	
8.1	INTRODUCTION.....	196
8.2	HABITAT HETEROGENEITY AND THE DIVERSITY OF LARGE HERBIVORES.....	197
8.3	VEGETATION DIVERSITY AND THE DIVERSITY OF LARGE HERBIVORES.....	203
8.4	VEGETATION BIOMASS AND LARGE HERBIVORE SPECIES RICHNESS.....	213
8.5	VEGETATION BIOMASS, SOIL FERTILITY AND WATER AVAILABILITY, AND THE BIOMASS OF LARGE HERBIVORES.....	214
8.6	SUMMARY.....	223
9.	DISCUSSION AND CONCLUSIONS	
9.1	INTRODUCTION.....	226
9.2	EVALUATION OF METHODS AND APPROACH.....	226
9.3	SYSTEM DYNAMICS AND THE DETERMINANTS OF DIVERSITY.....	231
9.3.1	Equilibrium and non-equilibrium theory.....	231
9.3.2	Determinants of system structure and diversity.....	235
9.3.2.1	Vegetation structure and diversity.....	236

9.3.2.2 Large herbivore biomass and diversity.....	262
9.4 CONCLUSIONS.....	271
9.4.1 Soils.....	271
9.4.2 Vegetation.....	272
9.4.3 Large herbivores.....	273
9.4.4 Diversity relations.....	274
10. LIST OF REFERENCES.....	275
Appendix 1 Soil summary statistics.....	295
Appendix 2 Soil classification.....	297
Appendix 3 Physiognomic classification of vegetation.....	304
Appendix 4 Regressions derived and calculation of moisture index.....	307
Appendix 5 Table of derived slope and intercept constants for predicting woody plant biomass.....	315
Appendix 6 Implications for management.....	320

LIST OF TABLES

	Page
1. Principal component analysis of soils.....	45
2. Woody plant name abbreviations used in figures.....	63
3. Coefficients of determination (r^2) between sample position on the first four principal components axes of soils and the first three detrended correspondence analysis axes of woody vegetation.....	65
4. Herbaceous plant name abbreviations used in figures.....	72
5. Mean mass and animal unit equivalents for large herbivores encountered in Mkuzi.....	97
6. Density (km^{-2}) of large herbivores in Mkuzi Game Reserve as estimated in August 1984.....	99
7. Biomass (kg km^{-2}) of large herbivores in Mkuzi Game Reserve as estimated in August 1984.....	101
8. Relative energy consumption expressed in animal units (AU) per unit area (km^{-2}) of large herbivores in Mkuzi Game Reserve as estimated in August 1984.....	102
9. Summary of the numbers, relative (AU) and proportional energy consumption (%) shot in and around Mkuzi during the second game eradication campaign (March 1943 to February 1950).....	106
10. Late dry and wet season herbaceous biomass and standing crop estimates (g m^{-2}) for the fifteen intensive study sites.....	139
11. Late dry and wet season utilizable woody plant biomass and total wet season woody plant biomass (g m^2) estimates for the fifteen intensive study sites.....	140
12. Correlation between 6 structural components of the vegetation, calculated from estimates of the proportion of the total biomass that each stratum comprised at each of 15 intensive sample sites.....	151

13. Estimated biomass (g m^{-2}), species richness (N_0) and equitability (E_c) of the large herbivore communities utilizing the fifteen intensive study sites in the late dry and wet seasons.....	160
14. Spearman rank correlation matrix for species richness and percentage cover within the major plant growth forms (woody plants, forbs and grasses). Data were from 0,1 ha sample sites.....	180
15. Derived coefficients (a and b) of the community richness and diversity (y) vs area (x) curves ($y-1 = ax^b$) used to derive relations shown in Fig. 65 and estimates of community richness (N_0 1000) and diversity (N_2 1000) for each site.....	198
16. Relation coefficients (r) between community richness (N_0 1000) and diversity (N_2 1000 and herbivore richness (N_0) and diversity (N_2) in the wet and dry seasons, and for the two seasons combined (Total N_0 and Mean N_2).....	199
17. Spearman rank correlation coefficients between habitat richness and diversity (abN_0 and abN_2 respectively) and large herbivore richness (N_0) and diversity (N_2) in the dry and wet seasons, and for the two seasons combined.....	201
18. Correlations (r) between the dry season indices of local diversity (N_0 , N_2 and E_c) for large herbivores and total utilizable vegetation.....	203
19. Correlations (r) between the wet season indices of local diversity (N_0 , N_2 and E_c) for large herbivores and total utilizable vegetation.....	204
20. Correlations (r) between the diversity of grazer and mixed feeder herbivores, and the diversity of herbaceous vegetation, grass and palatable grass in the dry and wet seasons.....	206
21. Correlations (r) between the diversity of grazing herbivores and the diversity of grass and palatable grass in the dry and wet seasons.....	211

22. Correlations (r) between the species richness of large herbivores and vegetation biomass. All correlations are for first degree polynomial curves, except for the wet season total vegetation biomass/herbivore richness comparison, which is linear..... 215
23. Correlations (r) between the biomass of vegetation and large herbivores..... 219
24. Major determinants of vegetation diversity and structure in Mkuzi and the spatial scales at which they are thought to be important..... 237

LIST OF FIGURES

	Page
1. Mkuzi Game Reserve location and drainage.....	4
2. Mkuzi Game Reserve climate diagram.....	6
3. Mkuzi Game Reserve rainfall isohyetal.....	7
4. Mkuzi Game Reserve, stratigraphy and topographic features.....	10
5. Geology of Mkuzi Game Reserve.....	13
6. Distribution of archeological sites.....	22
7. Distribution of old dwellings lands and stock pens.....	25
8. Principal component analysis of soil variates.....	46
9. Hierarchical cluster analysis of soils.....	48
10. Soil site ordination.....	49
11. Landtype soil ordination comparison.....	52
12. Species/area curves for trees.....	55
13. Species/area curves for shrubs.....	56
14. Influence of soils on vegetation physiognomy.....	59
15. Detrended correspondence analysis of woody plant species.....	62
16. Detrended correspondence analysis of woody plant stands.....	62
17. Comparison of soil and vegetation ordinations.....	66
18. Relations between vegetation ordination axes and selected soil variables.....	68
18. Relation between profile available moisture (P.A.M.) and the second woody plant ordination axis.....	69
19. Detrended correspondence analysis of herbaceous species.....	71
20. A comparison between two methods of woody plant classification.....	76
21. Vegetation classification with physiognomic, floristic and environmental summaries.....	78
22. Location of the thirteen ground transects in relation to five land types found in Mkuzi.....	95
23. Density of large herbivores in Mkuzi.....	100
24. Biomass of large herbivores in Mkuzi.....	100

25. Relative energy consumption by large herbivores in Mkuzi.....	103
26. Relative energy consumption of the six most important large herbivore species in each land type.....	103
27. Relative energy consumption values of large herbivore species culled in and around Mkuzi during the last nagana campaign (1943 - 1950).....	107
28. (a) Estimated densities of impala and (b) densities of impala removed from Mkuzi between 1950 and 1984.....	109
29. (a) Estimated densities of wildebeest and (b) densities of wildebeest removed from Mkuzi between 1950 and 1984.....	110
30. (a) Estimated densities of warthog and (b) densities of warthog removed from Mkuzi between 1950 and 1984.....	111
31. Estimated densities of (a) kudu and (b) zebra in Mkuzi between 1950 and 1984.....	113
32. Estimated densities of (a) giraffe and (b) white rhinoceros in Mkuzi between 1950 and 1984.....	114
33. Dominance diversity curves for large herbivores in Mkuzi	116
34. Principal component analysis of soils collected from the 15 intensive sites.....	142
35. Total utilizable biomass plotted against site position of the first principal component axis of soils.....	142
36. Utilizable woody biomass plotted against site position on the first principal component axis of soils.....	144
37. Herbaceous biomass plotted against site position on the first principal component axis of soils.....	144
38. The general relationship between major soil gradients as determined by principal components analysis and vegetation biomass a) to utilizable biomass, b) utilizable woody biomass and c) herbaceous biomass.....	145
39. The proportional and absolute vertical distribution of utilizable plant biomass at each of 15 sample sites representing different plant communities.....	148
40. Relative stem densities of all woody plants occurring in 0,5m height classes at two sites. a) illustrates a negative exponential continuous distribution and b) a bimodal distribution.....	153

41. Relative density of a) <i>Xeromphis rudis</i> (shrub with replacement) and b) <i>Rhus gueinzii</i> (Shrub with out replacement) in each of five height classes and measured at site 12.....	154
42. Size distribution of three trees with replacement. a) <i>Spirostachys africana</i> b) <i>Euclea divinorum</i> and c) <i>Euclea schimperii</i> and one without replacement d) <i>Acacia luederitzii</i> from site 4.....	154
43. Bimodal size class distributions of three tree species from different sites. a) <i>Ziziphus mucronata</i> site 7 b) <i>Acacia tortilis</i> site 6.....	155
44. Patterns of species relative importance from 15 intensive sample sites.....	157
45. Relation between equitability (E_c) and biomass of plant species biomass ($r = -0,586$, $0,05 > P > 0,01$).....	159
46. Relative abundance distributions of large herbivores at each intensive study site during the dry (a) and wet season (b) study periods.....	161
47. Relations between large herbivore species richness (N_o) and equitability (E_c), and biomass for dry and wet seasons.....	163
48. Detrended correspondence analysis trace for woody plants from 118 sample sites. a) Axis 1, b) Axis 2.....	168
49. Detrended correspondence analysis trace for herbaceous plants from 118 sample sites. a) Axis 1, b) Axis 2.....	170
50. Total plant species richness at each site in the ordination space created by the first two axes of the principal component analysis of soils.....	173
51. Mean and range of plant species richness from 0,1 ha sample sites against mean position of sample plots along the first (a) and second (b) axes extracted by the principal component analysis of soils.....	175
52. Mean and range of woody plant species richness from 0,1 ha sample sites against mean position of sample plots along the first (a) and second (b) axes extrated by the principal component analysis of soils.....	176

53. Mean and range of herbaceous plant species richness from 0,1 ha sample sites against mean position of sample plots along the first (a) and second (b) axes extracted by the principal component analysis of soils.....	177
54. Mean and range of grass species richness from 0,1 ha sample sites against mean position of sample plots along the first (a) and second (b) axes extracted by principal component analysis of soils data.....	178
55. Mean and range of forb species richness from 0,1 ha sample sites against mean position of sample plots along the first (a) and second (b) axes extracted by a principal component analysis of soils.....	179
56. Mean and range of species richness from 0,1 ha sample sites plotted against mean cover class estimate (a) woody plants, (b) forbs and (c) grass.....	182
57. Species richness plotted against utilizable wet season biomass for a) all plants and b) woody plants.....	182
58. Species richness plotted against reconstructed utilizable wet season biomass a) herbaceous, b) grass and c) forbs.....	184
59. Relations between dry season grass utilization and a) grass species richness (N_0) b) grass diversity (N_1) and c) forb species richness (N_0).....	187
60. Relation between forb species richness and the cumulative utilization of forbs measured at the end of the dry season.....	188
61. Relations between fire frequency and a) species richness (N_0) and b) equitability (E_c) of the herbaceous layer.....	191
62. Relation between fire frequency and the total biomass of woody plants.....	192
63. Relation between fire frequency and woody plant species richness.....	192
64. Relations between habitat diversity ($b_1(N_0)$) and a) total species richness (N_0) and b) dry season species (N_0) of large herbivores.....	202

65. Wet season large herbivore species richness vs total wet season utilizable vegetation diversity a) species richness (N_0), b) diversity (N_2) and c) equitability (E_c).....	205
66. Wet season grazer and mixed feeder species richness vs a) herbaceous layer species richness (N_0) and b) herbaceous equitability (E_c).....	207
67. Wet season grazer and mixed feeder species richness vs a) grass species richness (N_0), b) grass equitability (E_c) and c) palatable grass equitability (E_c).....	208
68. Relations between dry season grazer and mixed feeder N_2 diversity and a) N_2 diversity of palatable grass and b) equitability (E_c) of palatable grass.....	210
69. Relation between dry season grazer and mixed feeder equitability (E_c) and herbaceous species richness (N_0).....	210
70. Relations between the species richness of grazers and a) grass species richness (N_0), b) grass equitability (E_c) and c) palatable grass species richness (N_0) during the wet season.....	212
71. Relations between large herbivore species richness (N_0) and total utilizable vegetation biomass during the dry (a) and wet season (b).....	216
72. Relations between the dry season palatable grass biomass and the species richness of a) grazers and mixed feeders and b) grazers alone.....	217
73. Relations between the wet season palatable grass biomass and the species richness of a) grazers and mixed feeders and b) grazers and mixed feeders and b) grazers alone.....	218
74. Relations between grazer and mixed feeder biomass and a) herbaceous biomass and b) grass biomass during the wet season.....	220
75. Relations between the biomass of grazers and the biomass of a) grass and b) palatable grass in the wet season.....	221
76. Relations between the soil fertility gradient and a) total dry season large herbivore biomass and b) total wet season large herbivore biomass.....	222

77. The influence of land type diversity on gamma-diversity of Mkuzi.....	240
78. The influence of habitat diversity on beta-diversity and the land unit/community resolution.....	240
79. The influence of disturbance eg. selective grazing on beta-diversity at the land type-community resolution.....	243
80. Relation between soil nutrient status (total Exchangeable bases (TEB)), available moisture (mm) and woody production (gm^{-2}).....	247
81. Woody plant species richness (No) vs $\log_e$ total exchangeable bases (In TEB).....	248
82. Proposed connections between biotic and abiotic determinants and the species richness of woody plants at the community/patch scale.....	250
83. Relation between woody biomass and a) grass biomass ($r = -0,720(p < 0,01)$, for In woody biomass) and b) grass species richness (No) ($r = -0,806(p < 0,01)$), during the wet season.....	255
84. Proposed connections and relations between biotic and abiotic determinants of herbaceous species richness at the community/patch scale.....	256
85. Relation between woody biomass and a) forb biomass and b) forb species richness (No) ($r = -0,606(p < 0,05)$) during the wet season.....	259
86. Relation between grass biomass and a) forb biomass and b) forb species richness during the wet season.....	260
87. Conceptual model of plant availability to large herbivores....	267
88. Proposed connections and relations between biotic and abiotic determinants of large herbivore species richness at the habitat/stand scale.....	267

CHAPTER 1. INTRODUCTION

1.1 BACKGROUND AND GENERAL OBJECTIVES

Maintenance of biotic diversity is one of the primary aims of conservationists. Not surprisingly, therefore, the investigation of "ecological diversity" (Pielou, 1975) remains a central pursuit of both theoretical and applied ecologists.

The primary problem that preoccupies students of ecological diversity has been clearly stated by Pielou (1975), as follows: "given a stable many-species community, how have its constituent species come to share the same habitat and how do they maintain themselves and interact with one another? Hence what determines the number of species that can live together, and their relative proportions?"

In comparison with other continents, Africa has an extremely diverse mammal fauna (Coe, 1980). Of particular interest to tourists and ecologists alike, is the spectacular array of large mammals. Exponential human population growth in Africa, particularly in rural areas, and the extension and intensification of agriculture is rapidly diminishing the sizes of wildlife dominated areas which are now becoming islands in a sea of development.

Based on the theories of island biogeography (MacArthur and Wilson, 1967; Miller, 1978; Soule', Wilcox and Holtby, 1979; Harris, 1984; Wilcox, 1986) and without manipulative management, one would predict the loss of a proportion of the species present on the newly created islands. This is of extreme concern to conservationists and has continued to stimulate the drive to understand the determinants of diversity and the feasibility of manipulating these if necessary.

Besides the establishment of protected areas for the specific maintenance of species diversity, conservationists have attempted to justify the existence of wildlife outside these areas on the grounds that they would be more productive than domestic stock. Proponents of these wild multi-species utilization systems postulate that a diverse community of niche differentiated species use utilize the range resource more evenly than a single species system and should

therefore, produce more than the latter. Furthermore, it seems intuitive that much of the relative stability of populations in some communities is a consequence of species diversity, each species interacting in various ways to limit and stabilize one another's populations.

In view of the importance of these concepts to land use policies in a rapidly changing Africa, there is a need to examine them in more detail. The general aim of this study is to evaluate some hypotheses relating to diversity both at the primary and secondary producer levels, and to determine the nature of the diversity/biomass relations between the vegetation and large herbivores of Mkuzi Game Reserve.

1.2 APPROACH

A prerequisite for exploring diversity relationships is a basic description and understanding of the dynamics of Mkuzi Game Reserve. Since no a priori work of this nature had been undertaken, it was included in this study. As a result, the study divides into two main parts. The first is primarily descriptive and consists of background information on the study area (Chapter 2), a detailed investigation of the land types, soils and vegetation (Chapter 3) and a description of the large herbivore community structure and dynamics (Chapter 4).

The second part has as its aim the exploration of diversity relations. It starts with a review and discussion of hypotheses regarding diversity in ecological communities (Chapter 5), continues with a presentation of estimates of vegetation and herbivore biomasses at specific sites (Chapter 6). These data form the basis of many of the comparisons made between soils, vegetation biomass and vegetation diversity (Chapter 7), and vegetation and large herbivore diversity (Chapter 8). Chapter 9 discusses the results of Chapters 7 and 8, in the light of the hypotheses presented in Chapter 5.

CHAPTER 2. STUDY AREA AND DESCRIPTION

2.1 LOCATION AND SIZE

Mkuzi Game Reserve (latitude 27°30' to 27°45' south, longitude 32°05' to 32°25' east) is situated on the coastal plain east of the Lebombo Mountains in north eastern Natal (South Africa) and is approximately 40 km west of the coast (Fig. 1). It is bounded on the north and east by the Mkuze River, on the south by the Msunduzi River and on the west by a fenced boundary along the Lebombo Mountains (Fig. 1).

The reserve is approximately 290 km² in extent with a maximum length and width of 24 and 15 km, respectively. Altitude varies from 30 m above sea level in the extreme south-east to 480 m above sea level in the north-west.

2.2 CLIMATE

The climate of Mkuzi is described as warm to hot, humid sub-tropical (Schulze, 1965) and falls into Koppen's arid zone steppe climate group with a mean annual temperature of greater than 18°C (i.e. BSh). According to Thornthwaite's (1948) classification, Mkuzi is described as semi-arid with little or no moisture surplus in any season and having a megathermal thermal efficiency (i.e. Da'da').

The major climatic features are summarized in a climate diagram (Fig. 2) drawn according to Walter (1963). In general the average disposition of the sub-tropical high pressure zones and the intervening low pressure troughs, modified by local topography, are the determinants of climate in the area. The hot humid summer (mid-September to the end of March) includes the rainy season (Fig. 2). Rains are caused by the airstream circulating anticlockwise around the southerly situated Indian Ocean anticyclone. These north-easterly winds coming off the sea are moisture laden, more so than the south-westerly winds originating from the high pressure cell in the southern Atlantic Ocean.

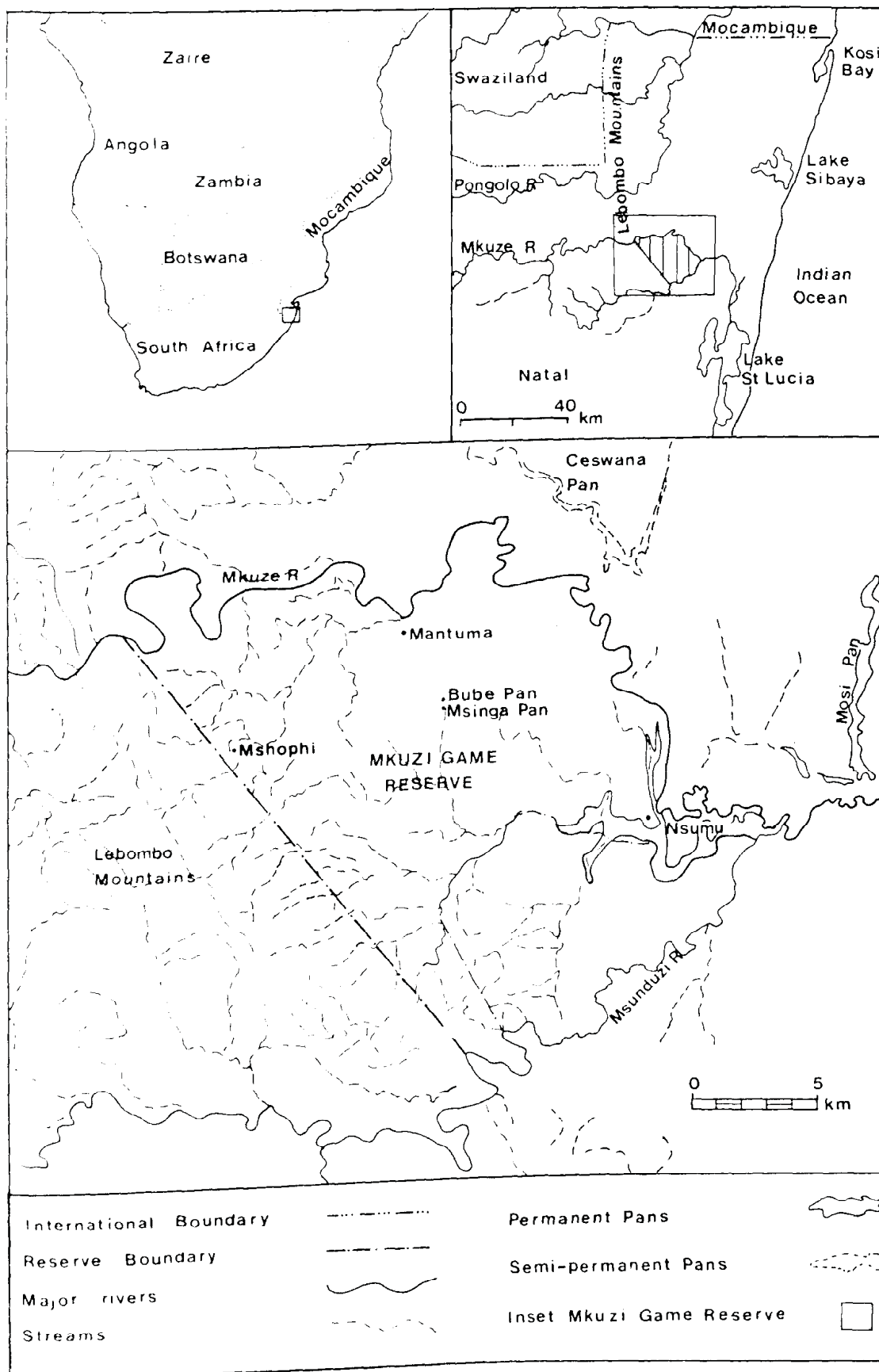


Fig.1 The location and drainage of Mkuzi Game Reserve.

During the warm arid winter (April to mid-September), the sub-tropical high pressure belt moves up over the southern African land mass, it being replaced by a semi-permanent winter-time continental anticyclone. Most of South Africa comes under the influence of the anticlockwise winds of this continental high. Spiralling outwards, the circulation is associated with divergence and subsidence; low level temperature inversions are common and smoke tends to accumulate beneath them. Dry hazy weather therefore prevails (Tyson, Preston-Whyte and Schulze, 1976).

In a semi-arid environment, the most important climatic factors are those that influence the moisture balance. These are primarily precipitation and evapotranspiration. Rainfall in and around Mkuzi is highly seasonal, peaking in February and with the month of lowest rain occurring in June (Fig. 2). The rainy season (all months with >50 mm of precipitation (Knoch and Schulze, 1957)) starts on average in October and ends in March (Goodman, 1981).

Spatial variation in annual rainfall within the reserve is not great, varying from c. 800 mm in the west to c. 600 mm in the east (Fig. 3). The longterm central tendency in rainfall as expressed by the mean for the weather station at Mantuma is 631 mm and when expressed by the median is 610 mm. Since the frequency histogram of annual rainfall is positively skewed (60% of observations occur below the mean), indicating a non-normal distribution, normal statistics are inappropriate expressions of rainfall central tendency and variability. In this instance the non-parametric median and associated measures of dispersion namely quartile, quintile and decile values provide a more realistic expression of central tendency and variability (Jackson, 1977; Simpson, Roe and Lewontin, 1960). The lower extreme and decile, upper decile and extreme values for the weather station at Mantuma are 345,3, 391,6, 849,2 and 1048,0 mm respectively. The quartile deviation is 126,4 mm and quartile deviation expressed as a percentage of the median is 20,7.

Greatest variability in the mean monthly rainfall received at Mantuma occurs during the dry winter months. This drops off markedly during spring and early summer, with the least variability occurring during November (Goodman, 1981).

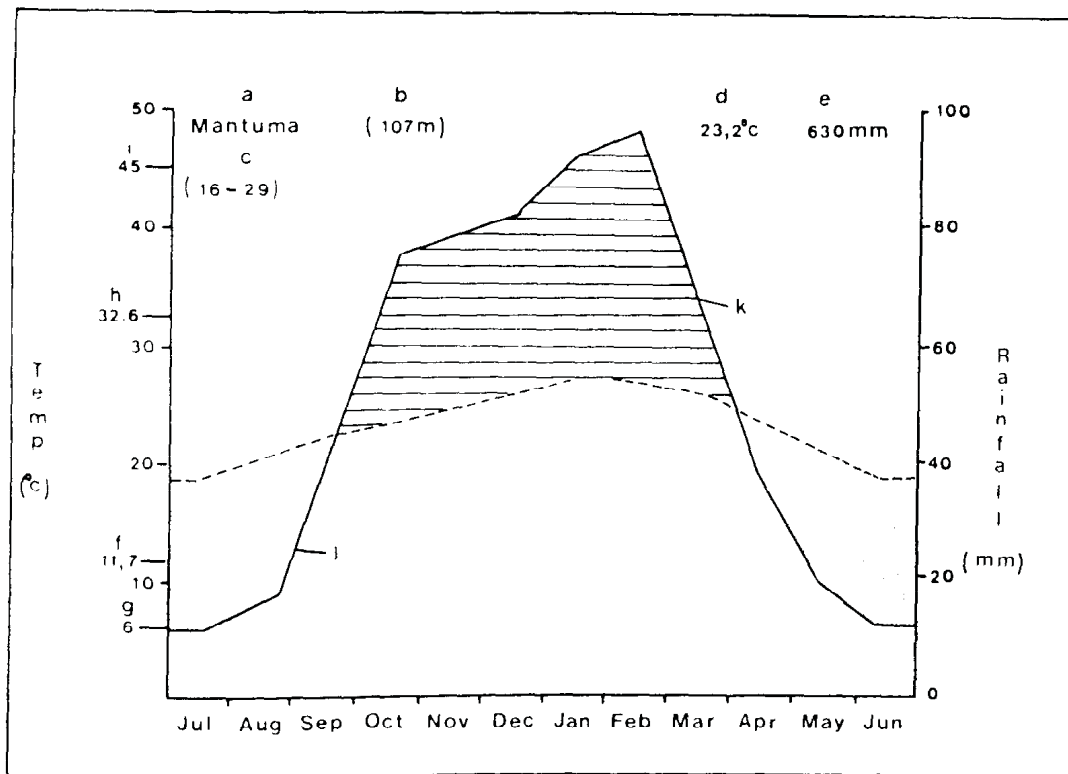


Fig 2 Climate diagram of Mkuzi Game Reserve. Monthly mean precipitation (—). Monthly mean temperature (---)

- a. Station name
- b. Altitude
- c. Number of years of observation temperature-precipitation
- d. Mean annual temperature
- e. Mean annual precipitation
- f. Mean daily minimum of coldest month °C
- g. Absolute minimum °C
- h. Mean daily maximum °C
- i. Absolute maximum °C
- j. Arid period (dotted area)
- k. Humid period (hatched area)

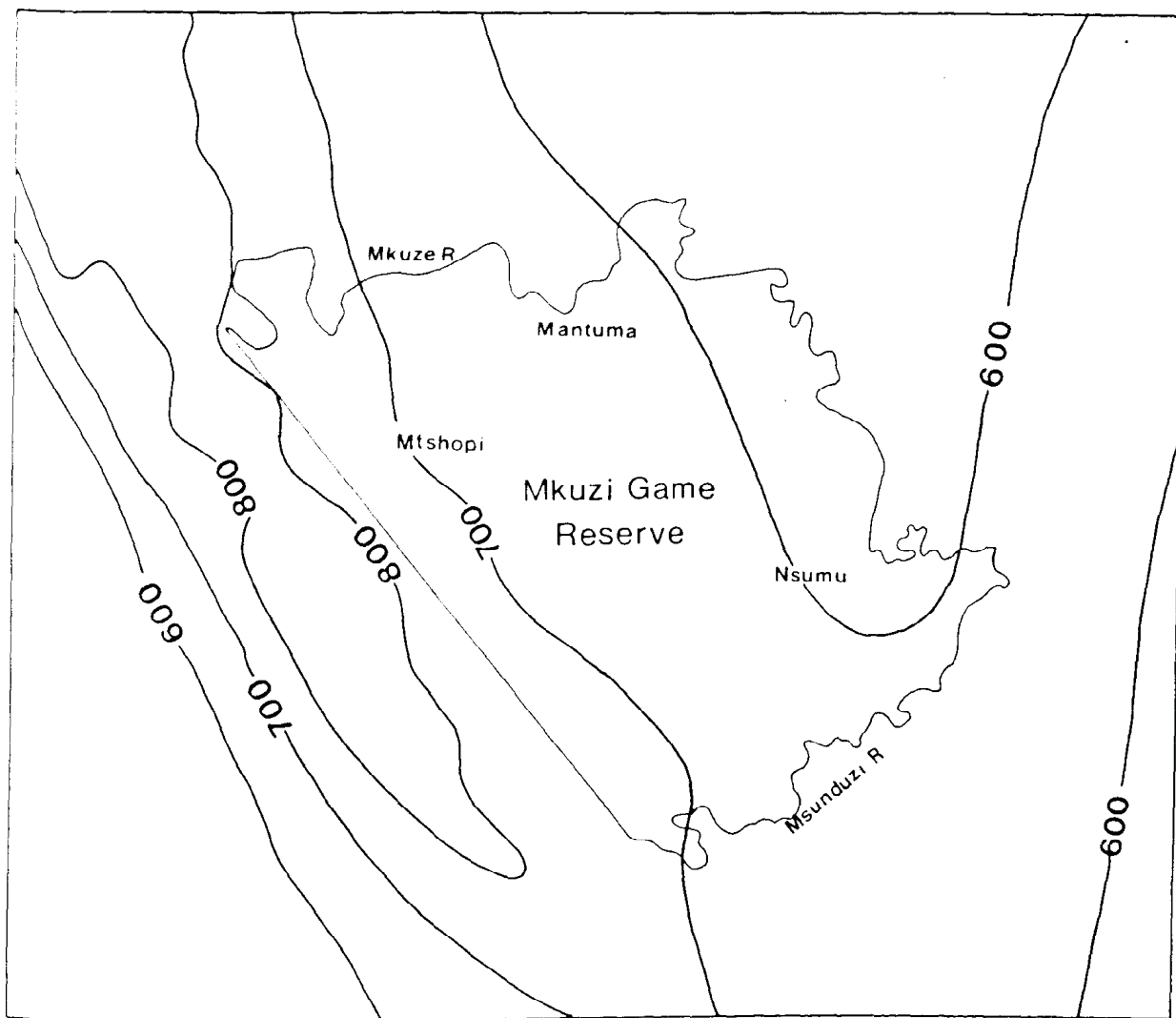


Fig.3 Isohyetal map for the study area.

Since shortly after the turn of the century, temporal variation in annual rainfall over south eastern Africa has experienced a weak underlying oscillation, producing a succession of extended wet and dry spells with a quasiperiodicity of about 18 years (Tyson, Dyer and Mametse, 1975; Tyson and Dyer, 1975; Dyer, 1976). It is stressed that this oscillation is only a component in the data which seldom accounts for more than 30 percent of the variance in annual rainfall, the remainder being random (Tyson and Dyer, 1975). The short term (30 years) rainfall records available from the weather station in Mkuzi were analysed using the same filter as Dyer (1976) and compared with his results (Goodman, 1981). The two patterns are similar with deviations which can possibly be accounted for by averaging in the regional analysis of Dyer (1976). The temporal behaviour of rainfall in this region appears to be related to the mean position of the subtropical high pressure belt (Dyer, 1979).

Short term estimates for pan evaporation are available from Mkuzi and longer term records are available from the Makatini Agricultural Research Station which is approximately 20 km north of the reserve and in the same bioclimatic region. Combined records from these two stations indicate a peak evaporative demand during December and January of approximately 230 mm per month. The month of lowest evaporative demand is June with a regional monthly mean of 110 mm. The mean annual pan evaporation for the region is 2100 mm.

In the absence of any actual measurements, evapotranspiration has been calculated by the method of Thornthwaite (1948). Estimated total annual potential evapotranspiration is 1230 mm, the peak occurring during January and the trough in June (Goodman, 1981). On average there is a moisture deficit in every month of the year, with an annual deficit of 599 mm.

The method of Thornthwaite (1948) estimates the rate of water use when water supply is non-limiting. That of Turc (1954 and 1955) attempts to account for the effect of a limiting water supply. Actual evapotranspiration calculated according to the method of Turc (1954 and 1955) is $606 \text{ mm annum}^{-1}$.

Mean annual temperature in Mkuzi is $23,2^{\circ}\text{C}$. Summers are hot, with the mean temperature for the hottest month being $27,1^{\circ}\text{C}$ and the mean maximum temperature for this month (January) being $32,5^{\circ}\text{C}$. The

absolute maximum temperature recorded to date is 45 °C (Fig. 2). Winters are warm with a mean daily temperature of 18,8 °C in the coldest month. The mean monthly minimum for the coldest month (July) is 11,7 °C with an absolute minimum for this month of 5,5 °C (Fig. 2). Frost has not been recorded at the weather station, but some signs of frosted plants have occurred in lower lying river valleys. The duration of the thermal summer (the time interval during which the monthly temperature curve lies above that of the mean annual temperature) in Mkuzi is approximately 183 days.

The prevailing winds in this area, and for the Natal coastal strip in general, are roughly north-easterly and south-westerly. The windiest period occurs during September and October, with the windiest month being September. The calmest month is June (Goodman 1981).

2.3 TOPOGRAPHY, GEOLOGY AND GEOMORPHOLOGY

The topography of the reserve is closely related to physiography and geology. Five land units are apparent within the reserve.

Occurring from west to east these are;

- i) the hilly Lebombo Mountains,
- ii) a gently undulating region underlain by Early Cretaceous sediments,
- iii) a gently, undulating, slightly, elevated Quarternary dune complex,
- iv) a low lying essentially flat region underlain by Late Cretaceous sediments and
- v) a low lying flat alluvial floodplain of recent origin which occurs adjacent to the two major rivers (Fig. 4).

The Lebombo Mountains consist predominantly of the Jozini Rhyolite Formation which overlies and post dates the more westerly occurring Sabi River Basalts (nomenclature according to Cleverly and Bristow, 1979) (Fig. 5). The Jozini formation is composed mainly of massive flows of rhyolite and rhyodacite interbedded with basaltic flows and several dykes, the most common of which are composed of dolerite. Acid dykes are also represented by simple and composite quartz-porphyry intrusions (Bristow, 1976). Rhyolite and rhyodacite