

https://dspace.org/

Classification of vegetation of the South African grassland biome

Ellery, William Nolan

1992

http://hdl.handle.net/10539/22708

Ellery, William Nolan (1992) Classification of vegetation of the South African grassland biome, University of Witwatersrand, Johannesburg, <http://wiredspace.wits.ac.za/handle/10539/22708>

Downloaded from a DSpace repository. https://dspace.org/

CLASSIFICATION OF VEGETATION OF THE SOUTH AFRICAN GRASSLAND BIOME

William Nolan Ellery

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 1992.

ABSTRACT

The aim of the study was to develop understanding of the relationships between vegetation types of the grassland biome of South Africa and the environment, with an emphasis on structural and functional characteristics.

The grassland biome in South Africa has traditionally been divided into 'pure' grasslands, assumed to be climatically determined, and 'false' grasslands of recent anthropogenic origin. A review of literature from several disciplines including palæobotany, archaeology, ecology and biogeography indicates that this is not a valid distinction. It is clear that the distribution of the grassland biome as a whole is poorly understood, but the general correlation between the distribution of biomes and climate elsewhere in the world suggests that this warrants more detailed investigation.

A water balance approach was used to develop climatic indices that both predict the distribution of grasslands, and are easy to interpret biologically. The indices are the mean number of days per annum when moisture is available for plant growth, the mean temperature on days when moisture is available for plant growth (wet season temperature), and the mean temperature when moisture is not available for plant growth (dry season temperature). Based on these three indices the grassland biome in South Africa can be distinguished from neighbouring biomes. The fynbos and succulent karoo biomes have rainfall in winter. The grassland, nama-karoo and savanna biomes have rainfall in summer. The forest biome experiences rainfall throughout the year. Of the summer rainfall biomes, the quantity of water available in the grassland biome is greater than in the nama-karoo, similar to savanna, but less than forest. Grasslands experience cooler dry season temperatures than savannas.

The localised distribution of woody plants within the grassland biome suggests that it is the effect of climate on the fire regime that may be of overriding importance in determining the distribution of the biome as a whole. Woody elements are restricted to sites that are either protected from fire, or experience fires of lower intensity than sites that support grassland. The unifying feature of the grassland biome is its proneness to fire. The presence of a warm, moist season promotes plant production and leads to a high standing crop close to the ground. The prolonged dry season

causes vegetation to dry out annually, rendering it flammable. More arid biomes have plants more widely spaced, making it difficult for fire to spread. In more mesic biomes where rainfall is less seasonal than in the grasslands or savannas, fuels do not dry out sufficiently to ignite. A number of additional climatic features may promote burning in the grassland biome. It has the highest lightning density of all South Africa's biomes. Warm, dry 'berg' winds desiccate fuels and promote burning in the more mesic grasslands. The 'curing' of the grass sward due to dry season frost and temperature drop is important in establishing early dry season flammability. Savanna trees are fire tolerant, but they appear sensitive to the cold temperatures prevalent in the grassland biome in the dry season.

The relationship between the distribution of functional characters of grassland plants and environmental conditions was investigated. The distinction between sweetveld, mixed veld and sourveld was recognised as one of the most important functional features of South Africa's grasslands. The distribution of these vegetation types was examined in detail. Sweetveld occurs in warm, dry areas; sourveld in cool, moist areas. There is overlap between these types that is dependant on soil nutrient status. Sweetveld that occurs in climatic conditions that would be expected to support mixed veld and sourveld, is on soils derived from basic parent material, including basalt, dolerite, gabbro and norite. Similarly, sourveld that occurs in areas that climatically would be expected to support sweetveld, is on soils derived from acid parent material such as sandstone and quartzite.

Soil nutrients that are most highly correlated to the occurrence of these three veld types are phosphorus availability and an index of nitrogen mineralization potential. There is an increase in both available phosphorus and the index of readily mineralizable nitrogen from sourveld to mixed veld to sweetveld. These features are incorporated into a conceptual model that relates the distribution of these grassland types to carbon and nitrogen metabolism, with the role of phosphorus either similar to nitrogen, or else it may act indirectly by affecting the rate of nitrogen mineralization. Nitrogen mineralization occurs at lower water availability than carbon assimilation, and its temperature optimum is higher than that of carbon assimilation. Where nitrogen mineralization is favoured relative to carbon assimilation, sweetveld is likely to occur. Where carbon assimilation is favoured relative to nitrogen

mineralization, sourveld is likely to occur. Soil texture affects the balance between these two processes in the degree to which it protects soil organic matter, and therefore the size of the nitrogen and phosphorous pools.

Changes in the distribution of South Africa's biomes for a scenario of climate change are predicted using the biome model developed in this study. This illustrates the value of developing predictive models.

DECLARATION

I declare that this thesis is my own, unaided work.
It is being submitted for the degree of Doctor of Philosophy
in the University of the Witwatersrand, Johannesburg.
It has not been submitted for any degree in any
other university.

W. Bellamy

17 day of December , 1992.

For Karen

PREFACE

Two unresolved issues in the grassland biome of South Africa intrigued me: why do we have grasslands; and why are some grasslands 'sweet' while others are 'sour'? The first issue is one which has puzzled ecologists dealing with similar vegetation elsewhere in the world. Conflicting theories have been advanced, specifically climate, fire and soils. As yet a single model has not been proposed to explain this phenomenon. The second issue, of 'sweet' and 'sour' veld may be a problem peculiar to South Africa's grasslands. The well entrenched functional terminology of 'sweetveld', 'mixed veld' and 'sourveld' reflects differences in the seasonal variation in forage quality between three distinct grassland types. What factors determine the distribution of these three vegetation units? Why does the forage quality in these grassland types vary seasonally? Why does sourveld become 'sweeter' following certain manipulations such as burning and fertilization?

I developed an interest in these particular aspects as I felt that they were attributes of vegetation that were broadly adaptive, and as such should be predictively related to the environment. In the face of global changes in climate, and in view of accelerated political and social change in the subcontinent of southern Africa, possibly with major changes in patterns of land-use and disturbance regimes, it seems appropriate to focus on aspects that will enable prediction. I hope in the thesis to develop an understanding of the distribution of the grassland biome, and of different grassland types, and to illustrate how this knowledge can be summarised for communication and prediction.

This endeavour was not undertaken alone. I will single out a few of the many who have contributed to the completion of this study. Dr M.T. Mentis and Dr R.J. Scholes initially suggested and motivated for a study of this type. Dr. M.T. Mentis contributed to its early development, but his departure half-way through the study left Dr R.J. Scholes to supervise the remaining work. I am endebted to both for their contributions; Dr R.J. Scholes in particular has been the catalyst of many ideas that are presented. Dr M.C. Scholes took over supervision for the final months. Members of the ecology lab as well as of the Resource Ecology Group (REG) have always taken an interest in the work, and provided a useful forum for discussion. Dr

E.R. Robinson and Prof. T.N. Huffman (Archaeology) have provided useful comment on draft manuscripts that have been submitted for publication. The final production of the thesis was greatly enhanced by facilities provided by Dr K. Balkwill and the University Herbarium. Tim and Alisoun House assisted with some of the tedium of data entry, and Alisoun drew some of the maps. Finally, Karen has been a great source of motivation and support, and her assistance throughout the study is acknowledged in a special way.

The Foundation for Research and Development (FRD) supported the study financially.

TABLE OF CONTENTS

ABSTRACT ii

PREFACE vii

LIST OF FIGURES xiv

LIST OF TABLES xviii

CHAPTER 1 INTRODUCTION

1.1 OBJECTIVES 1
1.2 RATIONALE 2
1.3 OVERVIEW: EXAMPLES OF APPROACHES TO THE STRUCTURAL AND FUNCTIONAL CLASSIFICATION OF VEGETATION 2
1.3.1 WHAT IS A FUNCTIONAL CLASSIFICATION? 2
1.3.2 GLOBAL AND SUBCONTINENTAL SCALE 3
1.3.2.1 VEGETATION STRUCTURAL TYPES 3
1.3.2.2 PHOTOSYNTHETIC TYPES 4
1.3.3 LANDSCAPE AND COMMUNITY LEVEL 7
1.3.3.1 SAVANNA STRUCTURAL AND FUNCTIONAL CLASSIFICATIONS 7
1.3.3.2 GRASSLAND FUNCTIONAL CLASSIFICATIONS . . 7
1.3.4 LOCAL SCALE 8
1.3.5 MATCHING PURPOSE AND APPROACH 8
1.4 SUMMARY 9

CHAPTER 2 DEVELOPING FUNCTIONAL CONCEPTS OF THE SOUTH AFRICAN GRASSLAND BIOME

2.1 DEFINTITION OF A BIOME 10
2.2 DEFINITION OF THE GRASSLAND BIOME BASED ON LIFE FORM 11
2.3 THE DISTRIBUTION OF THE GRASSLAND BIOME 12
2.3.1 EARLY CONCEPTS 12
2.3.2 RECENT CONCEPTS 12
2.4 DETERMINANTS OF THE DISTRIBUTION OF THE GRASSLAND BIOME 19
2.4.1 THE CONVENTIONAL VIEW 19
2.4.2 THE ALTERNATIVE VIEW 19
2.4.2.1 PALAEOBOTANICAL EVIDENCE 21
2.4.2.2 ARCHAEOLOGICAL EVIDENCE 22
2.4.2.3 BIOGEOGRAPHICAL AND ECOLOGICAL EVIDENCE 24
2.4.3 IMPLICATIONS 26
2.5 GRASSLAND FUNCTIONAL TYPES 27
2.6 SUMMARY 27

CHAPTER 3 BIOTIC AND ABIOTIC FEATURES OF THE GRASSLAND BIOME

3.1 INTRODUCTION 30
3.2 GEOLOGY AND GEOMORPHOLOGY 30
3.3 SOILS 36
3.4 CLIMATE 40
3.4.1 SOLAR RADIATION 40
3.4.2 TEMPERATURE 41
3.4.3 MOISTURE AVAILABILITY 41
3.5 FIRE 42
3.6 FAUNA 44
3.7 HUMAN IMPACT 45
3.8 SUMMARY 46

CHAPTER 4 DEVELOPING PREDICTIVE UNDERSTANDING OF THE DETERMINANTS OF THE GRASSLAND BIOME

4.1 INTRODUCTION 48
4.2 METHODS 49
4.2.1 SELECTION OF CLIMATIC INDICES BASED ON OTHER STUDIES 49
4.2.2 USE OF INDICES DERIVED FROM THE WATER BUDGET MODEL 51
4.2.3 DATA ANALYSIS 54
4.3 RESULTS 54
4.3.1 USE OF DISCRIMINANT FUNCTION ANALYSIS AS A TOOL FOR THE SELECTION OF APPROPRIATE CLIMATIC VARIABLES 54
4.3.2 SELECTION OF VARIABLES 60
4.3.3 COMPARISON OF THE TWO SOUTH AFRICAN APPROACHES 69
4.4 DISCUSSION 69
4.4.1 THE BIOLOGICAL INTERPRETATION OF INDICES USED IN THIS STUDY 69
4.4.2 THE IMPORTANT FEATURES OF A GRASSLAND CLIMATE 71
4.4.3 THE ROLE OF ANTHROPOGENIC FACTORS 71
4.5 SUMMARY 73

CHAPTER 5 THE DISTRIBUTION OF WOODED PATCHES WITHIN THE GRASSLAND BIOME

5.1 INTRODUCTION 78
5.2 METHODS 79
5.2.1 COLLECTION OF DATA IN THE FIELD 79
5.2.2 SOIL ANALYSES 79
5.2.3 CLIMATIC MODELLING 81
5.2.4 DATA ANALYSIS 85
5.3 RESULTS 85

5.3.1 THE CLASSIFICATION OF VEGETATION UNITS 85
5.3.2 THE DISTRIBUTION OF WOODED PATCHES IN THE GRASSLAND BIOME 91
5.3.2.1 CLIMATE 91
5.3.2.2 SOILS 91
5.3.2.3 TOPOGRAPHY AND FIRE 97
5.4 DISCUSSION 101
5.4.1 WHY NOT TEMPERATURE ALONE? 101
5.4.2 A RE-EVALUATION OF THE IMPORTANCE OF CLIMATE IN DETERMINING THE DISTRIBUTION OF SOUTH AFRICA'S GRASSLANDS 103
5.4.3 CLIMATE AND FIRE IN OTHER BIOMES 105
5.4.4 WHAT ABOUT TOPOGRAPHY AND SOILS? 106
5.5 SUMMARY: A SYNTHESIS OF THE ROLES OF CLIMATE AND FIRE 107

CHAPTER 6 IDENTIFYING THE MAJOR FUNCTIONAL FEATURES OF SOUTH AFRICA'S GRASSLANDS

6.1 INTRODUCTION 110
6.2 METHODS 110
6.2.1 VEGETATION SAMPLING AND SITE DESCRIPTION ... 110
6.2.2 CLIMATIC MODELLING 112
6.2.3 SOIL ANALYSES 112
6.2.4 DATA ANALYSES 113
6.2.4.1 INVESTIGATING RELATIONSHIPS BETWEEN SPECIES DISTRIBUTIONS AND ENVIRONMENTAL CONDITIONS 113
6.2.4.2 INVESTIGATING RELATIONSHIPS BETWEEN SPECIES DISTRIBUTIONS AND FUNCTIONAL CHARACTERISTICS 113
6.3 RESULTS 116
6.3.1 ORDINATION OF THE SPECIES BY STANDS MATRIX USING DETRENDED CORRESPONENCE ANALYSIS .. 116
6.3.2 ORDINATION OF FUNCTIONAL CHARACTERS 120
6.3.3 A SPECIES BASED FUNCTIONAL CLASSIFICATION OF GRASSLAND TYPES 120
6.3.3.1 GROWTH FORM CHARACTERISTICS 123
6.3.3.2 REPRODUCTION 123
6.3.3.3 PHYSIOLOGY 125
6.3.3.4 DEFENCE AND PALATABILITY 128
6.3.3.5 A PRELIMINARY FUNCTIONAL CLASSIFICATION: PROFILES OF SPECIES THAT OCCUR IN MOIST, INTERMEDIATE AND ARID AREAS 128
6.3.4 FOCUSING IN ON SWEETVELD, MIXED VELD AND SOURVELD 131
6.4 DISCUSSION: COMPARISON OF THIS APPROACH WITH OTHER APPROACHES 132

CHAPTER 7 TOWARDS PREDICTIVE UNDERSTANDING OF THE DETERMINANTS OF SWEETVELD AND SOURVELD

7.1 INTRODUCTION 135
7.1.1 THE DISTINCTION OF SWEETVELD AND SOURVELD . 135
7.1.2 AN HYPOTHESIS OF SWEETVELD AND SOURVELD DISTRIBUTION 138
7.1.2.1 THE RESOURCE AVAILABILITY HYPOTHESIS . 138
7.1.2.2 DETERMINANTS OF CARBON ASSIMILATION . 139
7.1.2.3 DETERMINANTS OF NITROGEN ASSIMILATION 140
7.1.2.4 INTERACTIONS BETWEEN CARBON AND NITROGEN ASSIMILATION 144
7.2 METHODS 146
7.2.1 MACROCLIMATE, GEOLOGY, AND THE DISTRIBUTION OF SWEETVELD, MIXED VELD AND SOURVELD . . . 146
7.2.2 INVESTIGATING THE IMPORTANCE OF MICROCLIMATE AND SOIL FERTILITY 146
7.2.2.1 VEGETATION SAMPLING AND SITE DESCRIPTION 146
7.2.2.2 DATA ANALYSES 149
7.3 RESULTS 152
7.3.1 DISCRIMINATION OF VEGETATION TYPES AT SUBCONTINENTAL SCALE: THE ROLE OF MACROCLIMATE AND PARENT MATERIAL 152
7.3.2 THE ROLE OF SOIL NUTRIENTS 160
7.3.3 PREDICTING THE DISTRIBUTION OF SWEETVELD, MIXED VELD AND SOURVELD 162
7.4 DISCUSSION 166
7.4.1 THE CARBON/NUTRIENT BALANCE AND THE DISTRIBUTION OF SWEETVELD AND SOURVELD . . . 166
7.4.2 TOWARDS A MECHANISTIC MODEL 168
7.4.3 IMPLICATIONS FOR THE SEASONAL CYCLE OF NITROGEN AND CARBON ASSIMILATION IN NATURAL GRASSLANDS 170
7.4.4 THE EFFECT OF CERTAIN MANIPULATIONS ON FORGAE QUALITY IN SOURVELD 171
7.5 SUMMARY 171

CHAPTER 8 SYNTHESIS

8.1 A SUMMARY OF THE STUDY 174
8.1.1 CLIMATE, FIRE, TOPOGRAPHY AND GRASSLANDS . . 174
8.1.2 DETERMINANTS OF THE DISTRIBUTON OF SWEET AND SOUR GRASSLAND TYPES 175
8.2 APPLYING THE MODELS: THE CONSEQUENCES OF A SCENARIO OF CLIMATE CHANGE FOR BIOME DISTRIBUTION 176

8.3 FUTURE RESEARCH 179
8.3.1 THE DISTRIBUTION OF THE GRASSLAND BIOME 179
8.3.2 THE DISTRIBUTION AND SEASONAL FORAGE QUALITY DYNAMICS OF SWEETVELD, MIXED VELD AND SOURVELD 179

REFERENCES 180

APPENDIX 1 CLIMATE STATIONS AND DATA USED IN THE DISCRIMINATION OF SOUTH AFRICA'S BIOMES 198

APPENDIX 2 SPECIES NAMES AND ABBREVIATIONS OF WOODY SPECIES USED IN THE CLASSIFICATION OF WOODY VEGETATION UNITS IN THE GRASSLAND BIOME 202

APPENDIX 3 FUNCTIONAL CHARACTERS AND ATTRIBUTES FOR EACH CHARACTER 203

APPENDIX 4 ATTRIBUTE SCORES FOR EACH FUNCTIONAL CHARACTER FOR EACH GRASS SPECIES USED TO IDENTIFY FUNCTIONAL FEATURES OF SOUTH AFRICA'S GRASSLAND BIOME 204

APPENDIX 5 SPECIES AND SAMPLE SCORES FOR THE FIRST FOUR AXES OF THE ORDINATION OF GRASSLAND VEGETATION IN THE GRASSLAND BIOME 208

LIST OF FIGURES

Figure 1.1: The classification and distribution of South Africa's biomes 6

Figure 2.1: The distribution of Acock's (1975) 'pure' and 'false' grassland types 15

Figure 2.2: Early view of the distribution of Iron Age people in South Africa 20

Figure 2.3: The distribution of Early, Middle and Late Iron Age settlement sites in South Africa 23

Figure 2.4: An analysis of terminology used by Acocks (1975) in reference to veld types in the grassland biome 28

Figure 3.1: The distribution of the grassland biome in South Africa 31

Figure 3.2: The geology of the grassland biome 34

Figure 3.3: Erosion surfaces and dissected areas of the grassland biome ... 38

Figure 4.1: The distribution of weather stations used to discriminate South Africa's biomes on the basis of climatic indices 50

Figure 4.2: The water balance model used to generate indices of growth days, growth temperature, and no-growth temperature 53

Figure 4.3: The distribution of weather stations in relation to mean annual rainfall and mean number of days of growth opportunity 59

Figure 4.4: The distribution of the weather stations in relation to the temperature during the growth and no-growth seasons 62

Figure 4.5: The distribution of weather stations in the summer rainfall biomes (plus forest) in relation to the temperature during the no-growth season and the duration of the growth season 63

Figure 4.6: The distribution of weather stations in the winter rainfall biomes (plus forest) in relation to the temperature during the no-growth season and the duration of the growth season 64

Figure 4.7: The distribution of weather stations in relation to the difference in temperature between the growth and no-growth seasons, and the duration of the growth season 66

Figure 4.8: A decision tree used to discriminate South Africa's biomes on the basis of climatic indices 67

Figure 4.9: The approximate distribution of Acock's (1953) False Upper Karoo 72

Figure 4.10: The distribution of weather stations in the summer rainfall biomes as well as the False Upper Karoo in relation to the temperature during the no-growth season and the duration of the growth season .. 74

Figure 4.11: Decision tree depicting the discrimination of nama-karoo from savanna and grassland 75

Figure 5.1: The distribution of study areas in which the distribution of woody plants was studied within the grassland biome 80

Figure 5.2: Techniques used to determine local site climatic conditions ... 82

Figure 5.3: Water balance model (including the effects of soil moisture properties) used to generate the indices of growth days, growth temperature and no-growth moisture properties 83

Figure 5.4: Hierarchichal classification of stands derived from the TWINSPAN cluster analysis 86

Figure 5.5: The distribution of sites in the grassland biome with and without woody plants in relation to the duration of the growth season and the temperature during the no-growth season 92

Figure 5.6: The distribution of sites in the grassland biome with and without woody plants in relation to the duration of the growth season and the temperature during the growth season 93

Figure 5.7: The distribution of sites in the grassland biome with and without woody plants in relation to the duration of the growth season and the slope 100

Figure 5.8: The fire exclosure plot at Thabamhlope in Natal 102

Figure 5.9: Conceptual model of the distribution of grassland and wooded vegetation units 108

Figure 6.1: The distribution of study areas within the grassland biome in which functional features of grassland plants were examined in relation to the environment 111

Figure 6.2: Schematic illustration of the way in which a stands by functional characters matrix was produced 115

Figure 6.3: The first two axes of the ordination of species and stands by detrended correspondence analysis 119

Figure 6.4: Comparison of the ordination of stands with important features of climate 121

Figure 6.5: Ordination of growth form characteristics based on the geometry of the species based ordination 124

Figure 6.6: Ordination of reproductive characteristics based on the geometry of the species based ordination 126

Figure 6.7: Ordination of physiological characteristics based on the geometry of the species based ordination 127

Figure 6.8: Ordination of defence (a) and palatability (b) based on the geometry of the species based ordination 129

Figure 6.9: The distribution of sourveld, mixed veld and sweetveld sites in relation to the first two axes of the species based ordination 133

Figure 7.1: Animal performance in sweetveld and sourveld over an annual cycle 136

Figure 7.2: Carbon assimilation in relation to moisture availability and temperature 141

Figure 7.3: Nitrogen mineralization in relation to moisture availability and temperature 142

Figure 7.4: An hypothesis of the determinants of sweetveld and sourveld in South Africa 145

Figure 7.5: . The distribution of weather stations used in this study to discrominate sweetveld, mixed veld and sourveld areas on the basis of climatic indices 147

Figure 7.6: The scheme used to classify sites as sour or sweet on the basis of species composition 151

Figure 7.7: The distribution of weather stations in sweetveld, mixed veld and sourveld areas in relation to the temperature during the growth and no-growth seasons, and the duration of the growth season 154

Figure 7.8: The mean values of selected climatic variables for sweetveld, mixed veld and sourveld 156

Figure 7.9: The distribution of weather stations in sweetveld, mixed veld and sourveld areas in relation to the temperature during the growth season and the growth minus the no-growth season temperatures 157

Figure 7.10: The distribution of a patch of sweetveld in the south-eastern Transvaal in relation to geology 159

Figure 7.11: The distribution of a patch of sweetveld in the central Transvaal in relation to geology 161

Figure 7.12: The distribution of stands in the grassland biome classified as sweetveld, mixed veld and sourveld in relation to the duration of the growth season, resin bag extractable phosphorus and an index of nitrogen mineralisation 164

Figure 7.13: A decision tree predicting the distribution of sweetveld and sourveld in relation to geology and climate 165

Figure 7.14: A conceptual model of determinants of grass forage quality . 169

Figure 8.1: Changes in the distribution of South Africa's biomes assuming a 2° C increase in temperature, and a 15% increase in rainfall 178

LIST OF TABLES

Table 1.1: Examples of botanical classifications emphasising characteristics that are of adaptive significance 5

Table 2.1: The broad-scale classification of grassland types recognised by early workers 13

Table 2.2: Classification of Acock's (1975) veld types that have been considered to occur in the grassland biome by various authors 16

Table 3.1: Stages in the geological development of southern Africa 33

Table 3.2: Stages in the geomorphological development of southern Africa . 37

Table 4.1: The climatic variables included in the stepwise discriminant function analysis to discriminate South Africa's biomes 55

Table 4.2: A summary of the stepwise discriminant function analysis of South Africa's biomes based on climate 56

Table 4.3: Pearson's correlation matrix of the climatic variables used in the discriminant function analysis of South Africa's biomes 58

Table 4.4: The success of the model discriminating the biomes of South Africa 68

Table 4.5: A comparison of error rates in the present study with the study of Rutherford and Westfall (1986) 70

Table 4.6: The success of the model discriminating the grassland, nama-karoo and savanna biomes assuming the grassland biome has been invaded by nama-karoo in the region of the False Upper Karoo 76

Table 5.1: Environmental variables determined for each study site in which the distribution of woody plants in the grassland biome was examined 84

Table 5.2: The species by stands matrix and basis for division of vegetation units as identified in the TWINSPAN classification 87

Table 5.3: Selected environmental conditions associated with each site visited in the study of the distribution of woody plants in the grassland biome 89

Table 5.4: The occurrence of sites with and without woody plants within the grassland biome in relation to soil type 95

Table 5.5: An analysis of stands that may be considered exceptions to the generally observed relationships between soils and the occurrence of woody elements 96

Table 5.6: The occurrence of wooded patches within the grassland biome on soils with an illuvial B-horizon 98

Table 5.7: Relationships between soil and topographical characteristics that influence fire frequency and intensity 99

Table 6.1: Environmental variables included in the species based ordination of stands in the functional classification of grassland types 114

Table 6.2: Eigenvalues and weighted correlation coefficients of environmental variables in the detrended correspondence analysis of species and sites 117

Table 6.3: Pearson's correlation coefficients of environmental variables included in the species based ordination 118

Table 6.4: The sums of canonical eigenvalues of the analyses of individual functional characters of grassland sites using principal components analysis and correspondence analysis 122

Table 6.5: Profiles of functional characters of grasses along a moisture gradient 130

Table 7.1: Variables included in the stepwise discriminant function analysis of climatic differences between sweetveld, mixed veld and sourveld 148

Table 7.2: Lists of species classified as sour, intermediate or sweet 150

Table 7.3: A summary of the stepwise discriminant function analysis of climatic variables 153

Table 7.4: The parent material of stations mapped as sweetveld, but that were predicted as being sourveld on the basis of climate 158

Table 7.5: A summary of the stepwise discriminant function analysis of microclimate and soil characteristics 163

Table 7.6: Indices of carbon assimilation, nutrient availability and nutrient indices as a fraction of an index of carbon assimilation 167

CHAPTER 1

INTRODUCTION

1.1 OBJECTIVES

The overall objective of this study was to develop predictive understanding of environmental determinants of vegetation of the grassland biome of South Africa, with an emphasis on structural and functional characteristics. This was approached at two scales of resolution. At the subcontinental scale biomes are defined on the basis of the dominant and co-dominant life-forms, and on climate (Rutherford & Westfall 1986). The distribution of South Africa's grassland biome may therefore be expected to be related to climate, although its origin and distribution are widely debated (Acocks 1975, Rutherford & Westfall 1986, Feely 1987). At a more detailed scale of resolution, different functional grassland types have been recognised within the grassland biome. These are referred to as sweetveld, mixed veld [1] and sourveld based on differences in their forage quality in various seasons (Acocks 1975, Tainton 1981, Zacharias 1990). Neither the distribution nor the causes of the observed differences in forage quality of these rangeland types are understood.

A second objective was to summarise understanding so that it can be communicated and used as a basis for prediction. The issue of global climate change is receiving widespread attention (Schlesinger 1989, Goodess & Palutikof 1992, Smith et al. 1992), and regional changes in patterns of land use and resource utilization in the face of social and political change in southern Africa are being widely debated (Cock & Koch 1991). This is indicated by the recent establishment of the International Geosphere-Biosphere Program with an emphasis on global geosphere-biosphere change, as well as the publication of the proceedings of a conference on geosphere-biosphere change in southern Africa (Shackleton 1990). Other publications such as Sunter (1987), Huntley (1989) and Huntley et al. (1989) illustrate the focus on regional and local issues.

---

[1] The Dutch *veldt*, now Afrikaans *veld* refers to the open country in the interior of southern Africa used for pasturage and farmland.

1.2 RATIONALE

Many studies have focussed on structural and functional features of vegetation that are considered to be of adaptive significance, and are therefore predictively related to the environment. The concept of 'life-forms' introduced by Raunkaier (1934) has proved to be of lasting value in the attempt to analyse the influence of macroclimate on vegetation composition. This system has been refined in the comprehensive system of Box (1981 a,b). The life-form approach is of great value in that it relies on morphological criteria readily applicable to all plant species. However, many important influences are not readily detectable by reference to morphology alone, and recent studies such as those of Grime (1977) and Noble & Slatyer (1979) reflect the continued effort to recognise additional plant attributes that have ecological function.

The classification of vegetation based on functional characteristics has been described as a functional classification (Grime 1985). It attempts to reduce the number of species taxa in floristically diverse vegetation types to a smaller number of functional types, each exhibiting characteristic structure and process. Despite floristic differences in forest, grassland and savanna on different continents for example, there are many intercontinental parallels in the structure and function of these vegetation types. In addition to making comparison and interpolation between widely separated study sites possible, functional classifications should enable prediction. The use of the plant taxa of conventional taxonomy for this purpose is at present unwieldy, and assumes that differences between taxa are greater than the variability within taxa. The sheer number of vascular plant species in South Africa (some 20 300; Siegfried 1989) presents daunting problems if they are to be used as a basis for understanding the response of vegetation to scenarios of change. Even if key species are chosen for a given area, problems of extrapolation remain.

1.3 OVERVIEW: EXAMPLES OF APPROACHES TO THE STRUCTURAL AND FUNCTIONAL CLASSIFICATION OF VEGETATION

1.3.1 WHAT IS A FUNCTIONAL CLASSIFICATION?

The emphasis in functional classifications is the clustering of items that exhibit similarity of process and occur under similar environmental conditions. An example

is that of the trophic guilds: producers, consumers and decomposers (Simberloff & Dayan 1991). This is contrasted with the Linnaean taxonomic classification which would produce a clustering of species not based on trophic type, but governed by assumed evolutionary relatedness. Heavy dependance in ecology on the Linnaean taxonomic system implicitly assumes that variation within species (normally assumed the fundamental unit of such classification systems) is less than between species. There are problems with this approach. An individual species may be poorly defined and it could have a number of functionally different sympatric forms (e.g. Themeda triandra). Alternatively, there may be several species that are functionally similar, making taxonomic-cladistic based classifications unnecessarily unwieldy. Nevertheless the taxonomic-cladistic system presently serves as a base classification for many functional classifications, whereby already named units are rearranged to suit ecological descriptive and predictive needs.

Several types of botanical functional classification already exist. Plant attributes that are selected in a study depend on the purpose of the study, and are scale related. A number of studies are described below, emphasising criteria that have been used, purposes, and appropriate spatial scales. It will be argued that despite the existence of numerous types of botanical functional classifications, other ones - not necessarily entirely novel - are needed.

1.3.2 GLOBAL AND SUBCONTINENTAL SCALE

1.3.2.1 VEGETATION STRUCTURAL TYPES

It has been common knowledge for several centuries that the broad-scale distribution of vegetation structural types, or 'biomes', is related to climate. This appears due to strong evolutionary convergence of growth-forms in phylogenetically unrelated plants growing in similar climates (Beard 1978). This relationship was used to describe and map the world's climate zones before extensive networks of weather stations were available. Structural units are embraced in the terms 'growth-form' and 'life-form', which here are regarded as synonomous despite arguments to the contrary (Beard 1978, Barkman 1988). Many authors use these terms interchangeably, recognising that function (emphasised in the 'life-form' concept) is related to

morphology (emphasised in the 'growth-form' concept). The life-form system developed by Raunkaier (1934) is one of the best known, based on the location of the perennating organ in relation to ground level (Table 1.1). Functionally it is related to the mode of survival during the unfavourable season. The life-form approach has been modified and improved, with Cain (1950), Braun-Blanquet (1965), Whittaker (1975) and Beard (1978) contributing to ideas on approaches to the structural classification of vegetation. This system continues to be refined as indicated by the recent publication of Barkman (1988) in which a new system of plant growth-forms has been proposed.

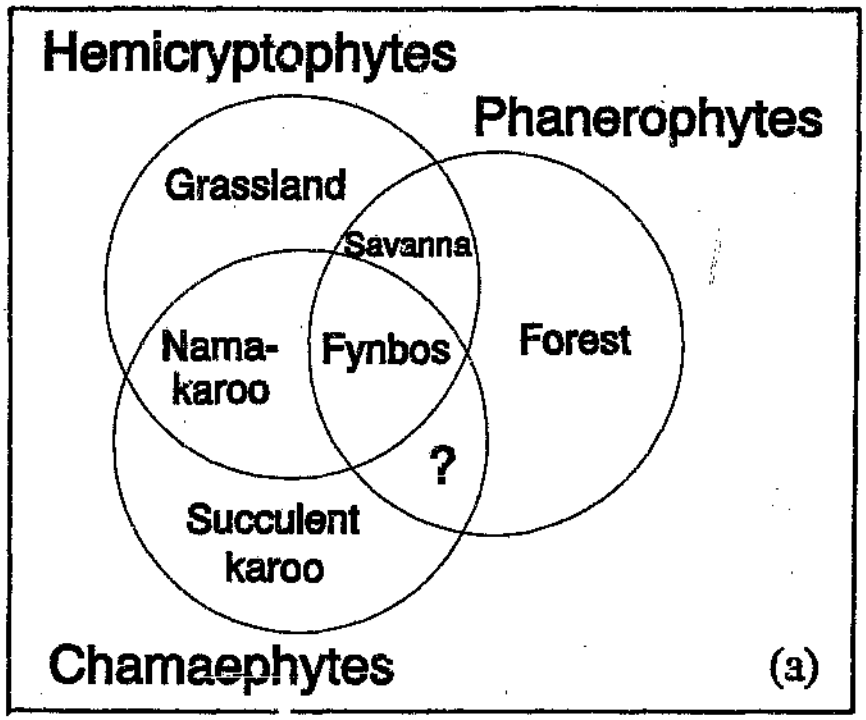
The life-form spectra of different vegetation types are used to indicate gross adaptation to climate (Raunkaier 1934). A system based on the dominance and co-dominance of different life-forms has been used to categorise South Africa's biomes objectively (Rutherford & Westfall 1986). The life-forms used to classify South Africa's biomes were: **hemicryptophytes**, with perennating buds at or close to ground level; **chamaephytes**, with perennating buds between ground level and 0.7 m; and **phanerophytes**, with perennating buds greater than 0.7 m above ground level (Rutherford & Westfall 1986). Six biomes, forest, fynbos, grassland, nama-karoo, savanna and succulent karoo (Fig. 1.1a) were recognised based on the dominance or co-dominance of one or more of the abovementioned life-forms (Fig. 1.1b).

1.3.2.2 PHOTOSYNTHETIC TYPES

Since the discovery of the C_4 photosynthetic pathway in the 1960's (Kortschack et al. 1965, Hatch & Slack 1966) there has been great interest in correlating the occurrence of this pathway with specific environmental conditions (Table 1.1). This has to some extent involved empirical correlation of macro-climatic variables with the distribution of C_3 and C_4 plants, of which there are many examples including Tieszen et al. (1979), Boutton et al. (1980), Rundel (1980), Teeri et al. (1980), Hattersley (1983), Collins & Jones (1985), Vogel et al. (1986) and Cavagnaro (1988). A number of studies in southern Africa have adopted a similar approach (Ellis 1977, Vogel et al. 1978, Ellis et al. 1980, Cowling 1983, Ellery et al. 1992). Altitude, moisture availability, temperature and the season of rainfall generally correlate well with the distribution of plants with different photosynthetic types, with few studies alluding to

Table 1.1: Examples of botanical classifications emphasising characteristics that are considered to be of adaptive significance and are therefore predictably related to habitat and ecology, the criteria on which they are based, their purpose and appropriate spatial scale. References are included numerically: 1 Raunkaier (1934); 2 Whittaker (1970); 3 Beard (1978); 4, 5 Box (1981a,b); 6 Rutherford & Westfall (1986); 7 Ellis (1977); 8 Vogel et al. (1978); 9 Tieszen et al. (1979); 10 Boutton et al. (1980); 11 Rundel (1980); 12 Ellis et al. (1980); 13 Teeri et al. (1980); 14 Cowling (1983); 15 Hattersley (1983); 16 Collins & Jones (1985); 17 Vogel et al. (1986); 18 Cavagnaro (1988); 19 Ellery et al. (1992); 20 Walter (1971); 21 Walker et al. (1981); 22 Walker & Noy-Meir (1982); 23 Johnson & Tothill (1985); 24 Frost et al. (1986); 25 Acocks (1975); 26, 27 Grime (1974, 1977); 28 Noble & Slatyer (1979).

CLASSIFICATION	CRITERION	PURPOSE	SCALE
Raunkaier's life-forms; (Refs. 1-6).	Location of perennating organ in relation to ground level.	Biological spectra indicate gross adaptation to climate.	Global and subcontinental.
Photosynthetic type; (Refs. 7-19).	Photosynthetic pathway, leaf anatomy.	Adaptation to macro- & micro-climate, nutrient availability.	Subcontinental and landscape.
Savanna functional classification (Refs. 20-24).	Woody - grass balance and woody leaf size & type.	Co-dominance of grasses and trees and different tree types.	Landscape.
Acocks's veld types (incl. sweet, mixed & sour); (Ref. 25).	Proportional species composition and seasonal forage quality.	ID regions with same farming potentiality, livestock production, veld management.	Landscape.
Grime's plant strategies; (Refs. 26, 27).	Degree to which competition, stress, disturbance constrain growth.	Describe life-history to index fitness for given conditions.	Local.
Noble & Slatyer's vital attributes; (Ref. 28).	Method of arrival, establishment, time to reach critical stages, persistence.	Predict replacement sequence of species following disturbance.	Local.



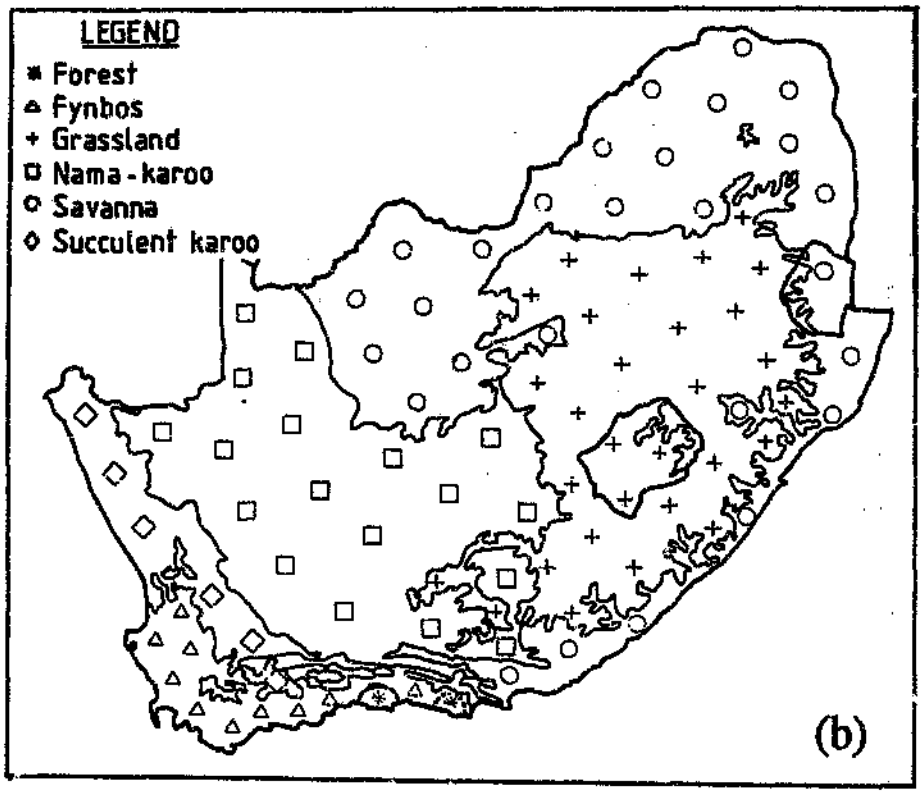


Figure 1.1: The classification of South Africa's biomes on the basis of the dominance and co-dominance of three life forms (a) and the distribution of these biomes (b; after Rutherford & Westfall 1986).

the effects of soil nutrient status (Cowling 1983, Ellery et al. 1992).

In contrast to this approach, many studies have adopted an experimental approach in which aspects of the performance of C_3 and C_4 plants have been related to specific environmental conditions, and this has been extrapolated to performance in nature. These studies have been reviewed by Pearcy & Ehleringer (1984), with predicted patterns from these studies generally agreeing with reported distribution patterns.

1.3.3 LANDSCAPE AND COMMUNITY SCALE

1.3.3.1 SAVANNA STRUCTURAL AND FUNCTIONAL CLASSIFICATIONS

Several approaches, varying from simple abiotic models to more detailed functional models (Table 1.1), have been used to develop predictive understanding of the distribution of structurally and functionally distinct vegetation types at regional scales, with work in savannas around the world being exemplary. The model of Walter (1971) can be considered a simple abiotic model. Access to soil moisture at different depths by trees (deep rooted) and grasses (shallow rooted) was related to rainfall, and was considered to explain the extent of woody plant development in savannas. This description was expanded to include two environmental gradients, rainfall and soil texture, once again predicting an increase in woodiness with increased moisture availability (Walker et al. 1981, Walker & Noy-Meir 1982). An additional model also based on moisture availability and soil texture has been proposed by Johnson & Tothill (1985), including the effects of soil waterlogging (cf. Tinley 1982). These models predict a decline in woodiness as moisture availability increases. More recent functional models predict the occurrence of different savanna functional types based on moisture availability and soil fertility (Frost et al. 1986).

1.3.3.2 GRASSLAND FUNCTIONAL CLASSIFICATIONS

In the classification of the veld types of South Africa (Acocks 1975; Table 1.1), terms were used that described structural and functional attributes of the vegetation. These included attributes related to the height of the sward and differences in seasonal variation in forage quality (sweetveld, mixed veld and sourveld) in the grassland

biome. In other biomes these included spinescence, scrubbiness, and succulence.

A further distinction between different grassland types in South Africa is between 'true' (climatically determined) and 'false' (anthropogenically induced) grasslands (Acocks 1975). Once again this distinction is the basis for different approaches to the management of rangeland within the grassland biome. The allegedly recent creation of the 'false' grasslands has been increasingly questioned in the literature (Mentis & Huntley 1982, Tainton & Mentis 1984, Feely 1987), and is reviewed in the light of information from a variety of disciplines in the following chapter.

1.3.4 LOCAL SCALE

The species-level taxon is commonly regarded to have a high degree of reality and a lesser degree of abstraction than taxa at higher or lower levels in the Linnaean system. Species are viewed as the units of evolution, and the units which make up vegetation. The aggregate behaviour of individual species represents the corporate response of a community to environmental conditions. The essence of this approach is to identify and understand the characteristics of individual species and their interactions with their cohabitors (Table 1.1). These viewpoints underpin the competit on-stress-disturbance models of Grime (1974, 1977), vital attribute models of Noble and Slatyer (1979), and life history and demographic studies such as MacArthur & Wilson (1967), van Valen (1971), Whittaker & Goodman (1979), and O'Connor (1991).

1.3.5 MATCHING PURPOSE AND APPROACH

Despite the existence of numerous types of botanical classifications, others are needed. A single all-purpose classification is improbable. Each is appropriate at a particular spatial scale, levels of resolution differ, and criteria are selected to match the purpose. It seems at this stage that an attempted combination of all of them into a single system would hamper the effort to understand, summarise, communicate and predict. The purpose of some existing classifications come close to or even overlap with the present study, which is to develop predictive understanding of the distribution of South Africa's grasslands, and to identify grassland types and

understand their distribution. Overall it appears that the ideal situation is to have several functional classifications specific to South African circumstances, and covering a range of spatial scales.

1.4 SUMMARY

The present study aims to develop predictive understanding of the distribution of South Africa's grasslands at two scales of resolution, the subcontinental and landscape. The study will emphasise structural and functional characters that are predictively related to habitat and ecology. A number of studies that have adopted similar starting points have been outlined, indicating their strengths for specific purposes and at different spatial scales. New approaches are needed to suit South African purposes, and to operate at different scales of resolution.

CHAPTER 2

DEVELOPING FUNCTIONAL CONCEPTS OF THE SOUTH AFRICAN GRASSLAND BIOME

2.1 DEFINITION OF A BIOME

Before developing a concept of the grassland biome itself, the concept of a biome needs to be defined. According to Rutherford & Westfall (1986) a biome is:

- the largest land community unit recognised at a continental or subcontinental scale;
- a unit mappable at a scale of no larger than 1:10 million;
- distinguished from other biomes primarily on the basis of dominant life form(s) in climax systems;
- distinguished from other biomes secondarily on the basis of major climatic features;
- not an unnatural or major anthropogenic system.

This definition is useful in that it addresses the issue of scale quite explicitly. The primary and secondary bases for distinguishing biomes however, pose some difficulties. For example, Rutherford & Westfall (1986) included the Afromontane vegetation of the highlands in Lesotho as part of the nama-karoo biome, based on the presence of a combination of hemicryptophytes and chamaephytes in both vegetation types (Rutherford & Westfall 1986). Although the physiognomy of these two vegetation types is similar, the climate that supports them appears different. Precipitation is higher in the Lesotho Highlands, and temperatures more variable (and cooler overall), than the nama-karoo (cf. Schulze & McGee 1978). Other studies elsewhere in the world frequently distinguish vegetation types on the basis of features other than physiognomy. For example, forests in North America are frequently divided into evergreen, deciduous, and coniferous, and grasslands into tallgrass and shortgrass (Whittaker 1975, Sowell 1985, Stephenson 1990). A similar approach may be necessary in South Africa to clarify the distribution of the nama-karoo and Afromontane vegetation of the Lesotho highlands.

A further problem with the definition is related to the stipulation that a biome is not an unnatural or anthropogenic system. Frequently it is difficult to determine whether a vegetation type has an anthropogenic origin or not. For example, Acocks (1975), in the most widely cited ecological publication in South Africa[1], attributed an anthropogenic origin to the much of the grassland biome of South Africa, based not on evidence of human activity in the region, but on the perceived existence of a 'climatic climax'. This suggestion is being increasingly questioned, and will be reviewed later in this chapter.

Despite these criticisms, the definition of the grassland biome of South Africa based primarily on life-forms and secondarily on climate appears satisfactory. The grassland biome will be defined on the basis of physiognomy in the following section. The issue of anthropogenic modification of much of the grassland biome will then be investigated in the form of a review of the literature, much of which has become available since Acocks first published his work in 1953.

2.2 DEFINITION OF THE GRASSLAND BIOME BASED ON LIFE FORM

The dominance and co-dominance of different life-forms has been used as the basis for distinguishing South Africa's biomes, with the grassland biome dominated entirely by hemicryptophytes (Rutherford & Westfall 1986). These are perennial plants, usually herbaceous, with perennating organs at or close to ground level, but seldom greater than 0.1m above ground level (Raunkaier 1934). The family Poaceae is the most widespread taxon with this growth form. Various authors have explicitly defined a 'grassland' as having less than a certain density (Phillips 1971) or cover of woody plants, this being between 2% and 5% cover (Pratt & Gwynne 1977, Edwards 1981). Having highlighted some of the problems associated with the biome concept, and having defined the grassland biome on the basis of physiognomy, what is the distribution of South Africa's grassland biome?

---

[1] Acocks's 'Veld types of South Africa' was first published in 1953. A second edition was published in 1975, and this was revised (only with species name changes) in 1988. The second edition will be referred to in the thesis, except where it differs from the first edition, in which case the first edition will be cited.

2.3 THE DISTRIBUTION OF THE GRASSLAND BIOME

2.3.1 EARLY CONCEPTS

There have been few broad-scale classifications of South Africa's grasslands. The first of note was by Bews (1918), who described the grasses and grasslands of South Africa. Within the vegetation type that he referred to as 'eastern grassveld', which approximates the present distribution of the grassland biome and much of the savanna biome (excluding the sandveld areas of the northern Cape and Botswana), he identified three types: the eastern grassveld itself; the coastal belt of Natal, and the mountain tussock grassveld (Table 2.1). Subsequently Bews (1929) published views on the grasses and grasslands of the world, dividing them into tropical and temperate units. Within each of these units he recognised types on the basis of grass height, and whether the grasses were predominantly tussock forming or not.

Pole Evans (1936) described grassland, forest, savanna ('parkland'), and desert shrub within South Africa. Within the grasslands, different types were distinguished based on plant height. Types were referred to as tall, short and mixed (Table 2.1), once again with little emphasis on floristic differences *per se*. This work was followed by a description of the major vegetation units of South Africa by Adamson (1938), with units approximating the present classification of biomes by Rutherford & Westfall (1986), namely sclerophyll, forest, grassland, savanna and semi-desert. Within the grassland biome, different types were recognised: including grassveld (highveld), dry grassland, moist grassland and montane (tussock) grassland (Table 2.1).

2.3.2 RECENT CONCEPTS

Acocks (1975) mapped the 'veld types' of South Africa explicitly based on the taxonomic-cladistic system. The veld types were grouped into broader vegetation units based on either biogeographical or structural affinity. His classification was implicitly based on the then-current ecological paradigm of succession (Weaver & Clements 1938). According to this theory, the climax is 'the highest expression of the vegetation in a climatic region' (Acocks 1964), and prevails except where disturbance has occurred, for example by grazing of domestic livestock and by fire.

Table 2.1: The broad-scale classification of grassland types recognised by different authors prior to Acocks (1953). As far as possible, the distribution of the types described by each author has been matched with the other authors.

Bews (1918)	Pole Evans (1936)	Adamson (1938)
Eastern grassveld	Short grass	Dry grassland
	Mixed grass	High veld
Coast belt of Natal	Tall grass	Moist grassland
Mountain tussock grassveld		Montane (tussock) grassland

Accordingly, Acocks (1975) recognised the grassy vegetation mostly to the west of the continental divide (his veld types 48 to 60) to be 'pure' in the sense that grassland there was thought to be the highest expression of the vegetation that the climate permitted (Fig. 2.1). To the east of the continental divide, Acocks (1975) also observed grasslands, despite, in his view, there being climate suitable (warmer in winter and wetter than to the west; Rutherford & Westfall 1986) for the development of 'higher' forms of vegetation, namely forest, scrub-forest and savanna. He explained the anomaly by invoking anthropogenic effects, implying that the former climax forests, scrub-forests and savannas of as little as 600 years ago had been reverted to disclimax or 'false' grasslands. They were considered to have been maintained by fire. Within this group he included his veld types 61 to 68.

In order to investigate the distribution of South Africa's grassland biome, a number of recent studies were compared. These studies have explicitly related the distribution of the grassland biome to Acocks's (1975) veld types. The most notable examples are Mentis & Huntley (1982), Huntley (1984), Tainton (1984) and Rutherford & Westfall (1986). A comparison of these classifications is presented in Table 2.2. There is agreement by all of these authors that Acocks's 'pure' grassveld types (veld types 48 to 60) are part of the grassland biome, except that Rutherford & Westfall (1986) classify Themeda-Festuca alpine veld (veld type 58) as being partly in the grassland biome and partly in the nama-karoo biome. Based on the review of the vegetation of the Afro-alpine region of southern Africa (Killick 1978) it appears that areas at high elevation in Lesotho support a short scrubby vegetation that is structurally related to nama-karoo (dominated by chamaephytes and hemicryptophytes). Based on this combination of life forms this area does not appear to be part of the grassland biome.

Areas included by Acocks (1975) as 'false' grassveld types (veld types 61 to 68) are included as part of the grassland biome in all four studies, with the exception that Rutherford & Westfall (1986) do not include the Pietersburg plateau grassveld (veld type 67) or Eastern province grassveld (veld type 68) as part of the grassland biome. Based on the incluson of these in the grassland biome in the majority of these studies, and on evidence from a detailed study in one these regions (cf. Stalmans 1990), these veld types are included in the grassland biome for the purposes of the present study.

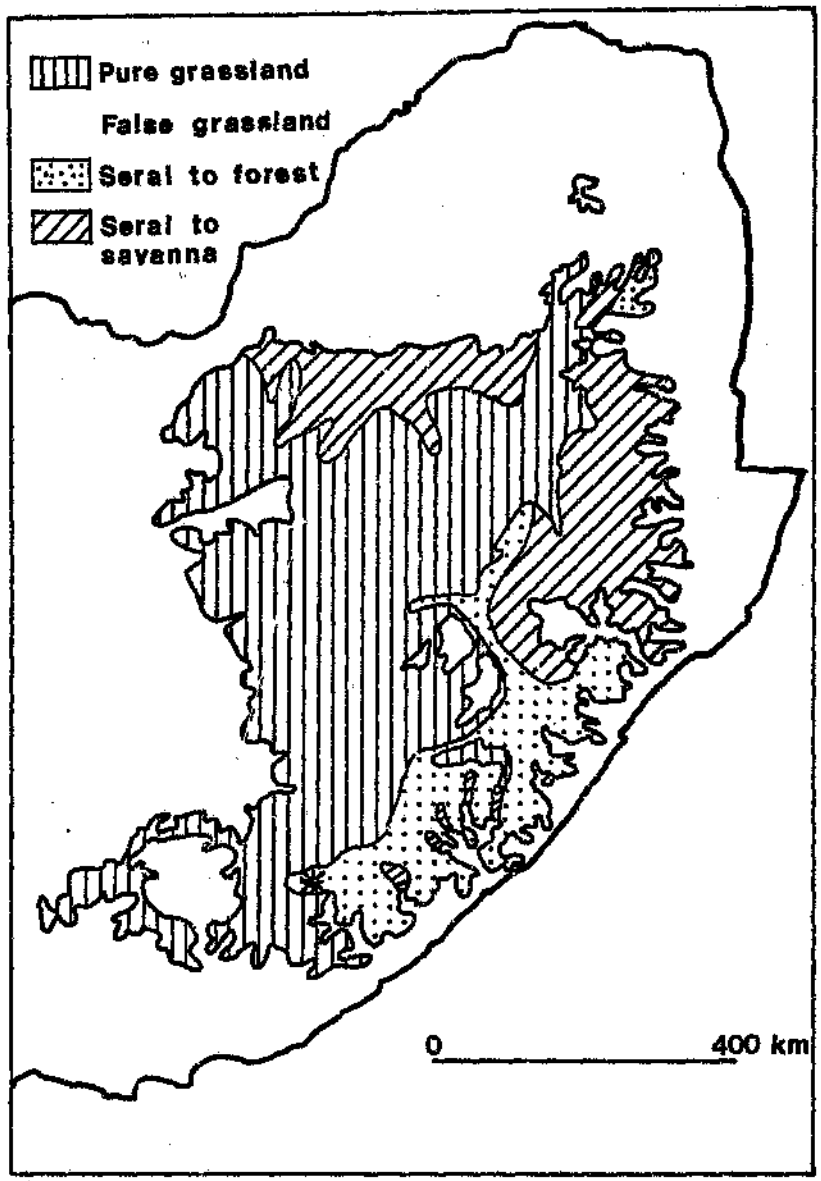


Figure 2.1: The approximate distribution of Acock's (1975) 'pure' and 'false' grasslands (after Mentis & Huntley 1982, Rutherford & Westfall 1986). The false grasslands were mapped as seral to forest and seral to savanna. The location of the Winterberg Mountains in the eastern Cape is indicated by an asterisk.

Table 2.2: Classification by (1) Mentis & Huntley (1982), (2) Huntley (1984), (3) Tainton (1984) and (4) Rutherford & Westfall (1986) of Acocks's (1975) veld types that have been considered to occur in the grassland biome. Classification into a biome other than the grassland biome (-), just the grassland biome (G), or a combination of grassland with forest (F), nama-karoo (N) and savanna (S) biomes are described. The broad-scale classification of vegetation by Acocks (1975) is provided as a heading for each block, and each veld type has tentatively been classified (Cn.) on the basis of these and other studies (see text).

No.	Veld Type	1	2	3	4	Cn.
	COASTAL TROPICAL FOREST					
1	Coastal forest and thornveld	G	GSF	G	-	-
3	Pondoland coastal plateau sourveld	G	GF	G	GS	G
5	'Ngongoni veld	G	GF	G	G	G
6	Zululand Thornveld	-	GSF	G	-	-
7	Eastern Province thornveld	-	GSF	G	-	-
	INLAND TROPICAL FOREST					
8	North-eastern mountain sourveld	G	GF	G	GS	GS
9	Lowveld sour bushveld	-	-	G	-	-
	FALSE BUSHVELD TYPES					
21	False thornveld of eastern Province	G	-	-	G	G
22	Invasion of grassveld by Acacia karoo	G	GS	-	-	-
	FALSE KAROO TYPES					
41	Pan-turf veld invaded by karoo	G	-	-	-	-
42	Danthonia mountain veld replaced by karoo	G	-	-	-	-
	TEMPERATE AND TRANSITIONAL FOREST AND SCRUB TYPES					
44	Highland sourveld and Dohne sourveld	G	-	G	G	G
45	'Ngongoni veld of Natal mist-belt	G	GF	G	G	G

Table 2.2 (cont.):

No.	Veld type	1	2	3	4	Cn
	PURE GRASSVELD					
48	Cymbopogon-Themeda veld	G	G	G	G	G
49	Transitional Cymbopogon-Themeda veld	G	G	G	G	G
50	Dry Cymbopogon-Themeda veld	G	G	G	G	G
51	Pan-turf veld	G	G	G	G	G
52	Themeda veld	G	G	G	G	G
53	Themeda veld to Cymbopogon-Themeda veld transition	G	G	G	G	G
54	Themeda veld to highland sourveld transition	G	G	G	G	G
55	Themeda veld to bankenveld transition	G	G	G	G	G
56	Highland sourveld to Cymbopogon-Themeda veld transition	G	G	G	G	G
57	North-eastern sandy highveld	G	G	G	G	G
58	Themeda-Festuca alpine veld	G	G	G	GN	GN
59	Stormberg plateau sweet veld	G	G	G	G	G
60	Karroid Danthonia mountain veld	G	G	G	G	G
	FALSE GRASSVELD TYPES					
61	Bankenveld	G	G	G	G	G
62	Bankenveld to sour sandveld transition	G	G	G	G	G
63	Piet Retief sourveld	G	G	G	G	G
64	Northern tall grassveld	G	G	G	G	G
65	Southern tall grassveld	G	G	G	G	G
66	Natal sour sandveld	G	G	G	G	G
67	Pietersburg plateau grassveld	G	G	G	-	G
68	Eastern province grassveld	G	G	G	-	G

A number of veld types were suggested by Acocks (1975) to be grassland, but have been invaded by either karroid elements or by thorn trees. Veld types considered grasslands that have been invaded by karoo are the Pan-turf veld invaded by karoo (veld type 41), and Karoid Merxmuellera mountain veld (veld type 42). Those considered grassland invaded by thorn trees are the False thornveld of the eastern Cap[illegible] type 21), and Invasion of grassland by thorn (veld type 22). According to Acocks (1975), all of these units are the result of excessive grazing pressure associated with modern systems of animal production, and are therefore anthropogenic. If they are of anthropogenic origin, these veld types should be included in the grassland biome as suggested by Mentis & Huntley (1982), but in the absence of any published information on the recent vegetation history of these areas, the classification of Rutherford & Westfall (1986) will be adhered to. A further veld type that was mapped by Acocks (1975) as grassland invaded by karoo is the False upper karoo (veld type 36). This was not included in any of the recent studies as part of the grassland biome, although its status is considered in detail by Rutherford & Westfall (1986), who include it in the karoo biome. It is the subject of ongoing study (Hoffman & Cowling 1990), and is worthy of more detailed investigation from the point of view of whether change has taken place there or not, and if so, the cause of change.

Two veld types east of the continental divide that are considered by all of the authors except Huntley (1984) to be grassland are Highland sourveld and Dohne sourveld (veld type 44) and 'Ngongoni veld of Natal mist-belt (veld type 45). These are both included as part of the grassland biome in this study.

Only two of the remaining veld types that were considered in recent biome-wide studies are thought to belong entirely to the grassland biome. These are the Pondoland coastal plateau sourveld (veld type 3) and Ngongoni veld (veld type 5). Shackleton (1989) studied part of the Pondoland coastal plateau sourveld in detail and was of the opinion that it should be mapped as part of the grassland biome. For the remaining veld types presented in Table 2.2, Rutherford & Westfall's (1986) classification is deemed appropriate. The veld types that ought to be included in the grassland biome are summarised in the final column of Table 2.2.

2.4 DETERMINANTS OF THE DISTRIBUTION OF THE GRASSLAND BIOME

2.4.1 THE CONVENTIONAL VIEW

The traditional view is that Acocks's (1953) 'pure' grasslands are climatically determined, but that his 'false' grasslands are of anthropogenic origin and that they are maintained by fire (Tainton 1981). At the time of Acocks's (1953) initial proposal, Bantu speaking people were thought to have inhabited much of the interior highveld as well as much of the east coast and its interior for many centuries (Fig. 2.2). This view was based largely on the work of Stow (1905), and was prevalent for many decades thereafter (Soga 1932, Krige 1936).

According to Rutherford & Westfall's (1986) definition of a biome, that it is the climax and not an unnatural or major anthropogenic unit, the 'false' grasslands should not be included in the grassland biome. Although Rutherford & Westfall (1986) reject the proposed anthropogenic origin of the false grasslands, and include them as part of the grassland biome, their discrimination of the grassland biome was poor. In their attempt to discriminate grassland and savanna, there was an error rate of 33% for those weather stations situated in the vegetation mapped by Acocks (1975) as grassland seral to forest or scrub forest.

The distinction between 'pure' and 'false' grasslands in South Africa has been increasingly questioned based on recent evidence (Ellery & Mentis in press). This is presented in the following section as an alternative view.

2.4.2 THE ALTERNATIVE VIEW

It has been suggested that the grassland biome as it is known today, (including the 'pure' and the 'false' grasslands), was in existence prior to the settlement of the subcontinent by Iron Age farmers and European settlers (Feely 1987), and that its origin is not as recent as suggested by Acocks (1975). Since the 1950's studies in a variety of disciplines including palaeobotany, archaeology, biogeography and ecology have improved our understanding of the age of the grassland biome as a whole. This information suggests that the grassland biome as it is presently mapped (including the

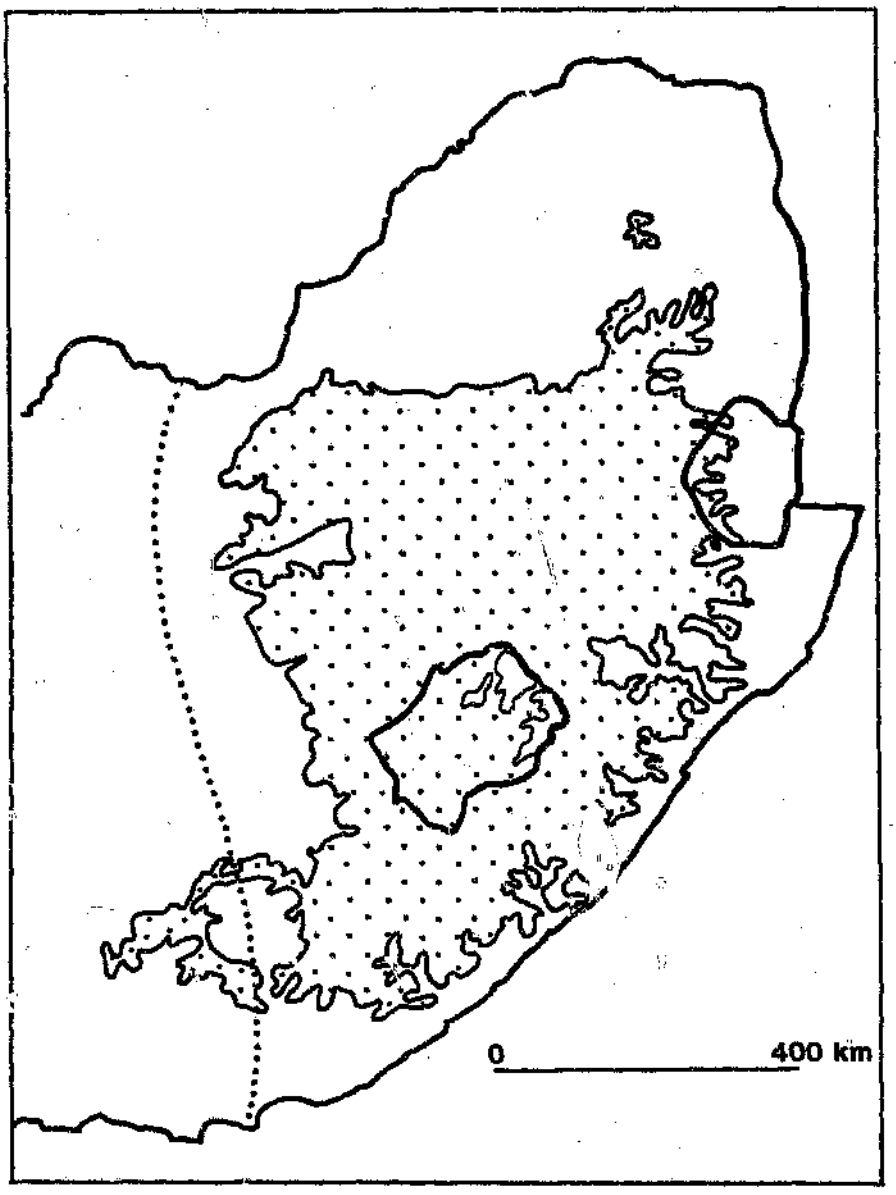


Figure 2.2: A map illustrating the early view of the approximate western limit (dotted line) of the distribution of Iron Age people (after Stow 1905, Soga 1930, Krige 1936), superimposed on a map of the grassland biome (stippled).

'false' grasslands) is considerably older than the 600 years suggested by Acocks (1975), making it necessary to reconsider the determinants of the distribution of the grassland biome as a whole.

2.4.2.1 PALAEOBOTANICAL EVIDENCE

Palaeobotanical studies would provide the most useful test of Acocks's (1975) suggestion that during the last 600 years there has been widespread destruction of forest east of the continental divide, yet little work has been done in this regard. The vegetation history of the Winterberg mountains in the eastern Cape (Fig. 2.1), in an area considered to be seral to forest (Acocks 1975), has been described for approximately the last 12 000 years based on pollen analyses from organic sediments (Meadows & Meadows 1988). Throughout the period covered by cores taken at two sites, pollen from the Poaceae and Cyperaceae has been dominant, suggesting that vegetation similar to that in existence today has been predominant throughout the period of organic accumulation (Meadows & Meadows 1988). During the period from approximately 12 000 BP to 8 000 BP the grassland flora contained more xeric elements than at present. Montane forest elements appeared for the first time approximately 8 000 BP, at which time the presence of xeric elements declined. Throughout the remaining period the forest elements appear to have been present in small quantities, suggesting a mosaic similar to the one that exists in the region at present, although sediments from the last few hundred years show signs of more intensive agriculture and disturbance (Meadows & Meadows 1988).

Based on this evidence Meadows & Meadows (1988) suggest that the montane forest communities of the Winterberg have not expanded much beyond their present-day patches during the last 12 000 years. Archaeological studies indicate that the Winterberg area had not been exploited by agropastoralists until occupation by European settlers during the last 200 years. Prior to that it may have been inhabited by hunter-gatherer communities (Hall 1986) whose impact on the vegetation was probably small.

A further study on the grasslands of the Nyika plateau in Malawi, also considered seral to forest (Chapman & White 1970, White 1983) reveals that the grasslands

there have been in existence for at least 12 500 years (Meadows 1983), which once again is considerably longer than they have been occupied by Iron Age Bantu speaking people. Meadows (1983) therefore suggested that this was also a stable vegetation type, and recognised that its distribution was poorly understood.

2.4.2.2 ARCHAEOLOGICAL EVIDENCE

Acocks (1975) believed that much of the grassland biome was inhabited by Bantu speaking farmers in the period before the arrival of white settlers. These Iron Age people relied on the use of wood for many of their activities, including the construction of semi-permanent villages and the production of pottery and metal products (Maggs 1984, Hall 1987). Historiographic and archaeological studies since the 1950's indicate that the immigration of these people into the subcontinent was a much more recent phenomenon than was previously considered the case. An understanding of their patterns of immigration provides strong circumstantial evidence that the grassland biome as it is presently distributed has been in existence for much longer than it has been inhabited by Iron Age people.

The first Iron Age people settled in the subcontinent in about 250 AD. At that time Iron Age settlement sites were mainly east of the great escarpment (Fig. 2.3). The distribution of sites shows a clear relationship with environmental conditions. Prior to 500 AD they were all located within relatively close proximity to the coast, on dunes that would appear to have supported forest (Maggs 1984, Feely 1987). Within these areas there is little evidence of any activity in the surrounding grasslands (Feely 1987). Subsequent immigration into the Transvaal from the north and north-west during the Middle Iron Age (up to between 900 and 1 000 AD) extended as far south as the present northern limit of the grassland biome (Fig. 2.3). In the Transvaal, sites were situated beside permanent rivers and on colluvial soils which would have supported agriculture. In Natal there was some movement to the interior at much the same time, from settlements further east, into the hot, dry, incised valleys of larger rivers in the areas presently mapped as valley bushveld by Acocks (1975). These sites were probably associated with a mixed bushveld vegetation (Maggs 1984).

At about 1 000 to 1 200 AD the distribution of Iron Age settlement sites was confined

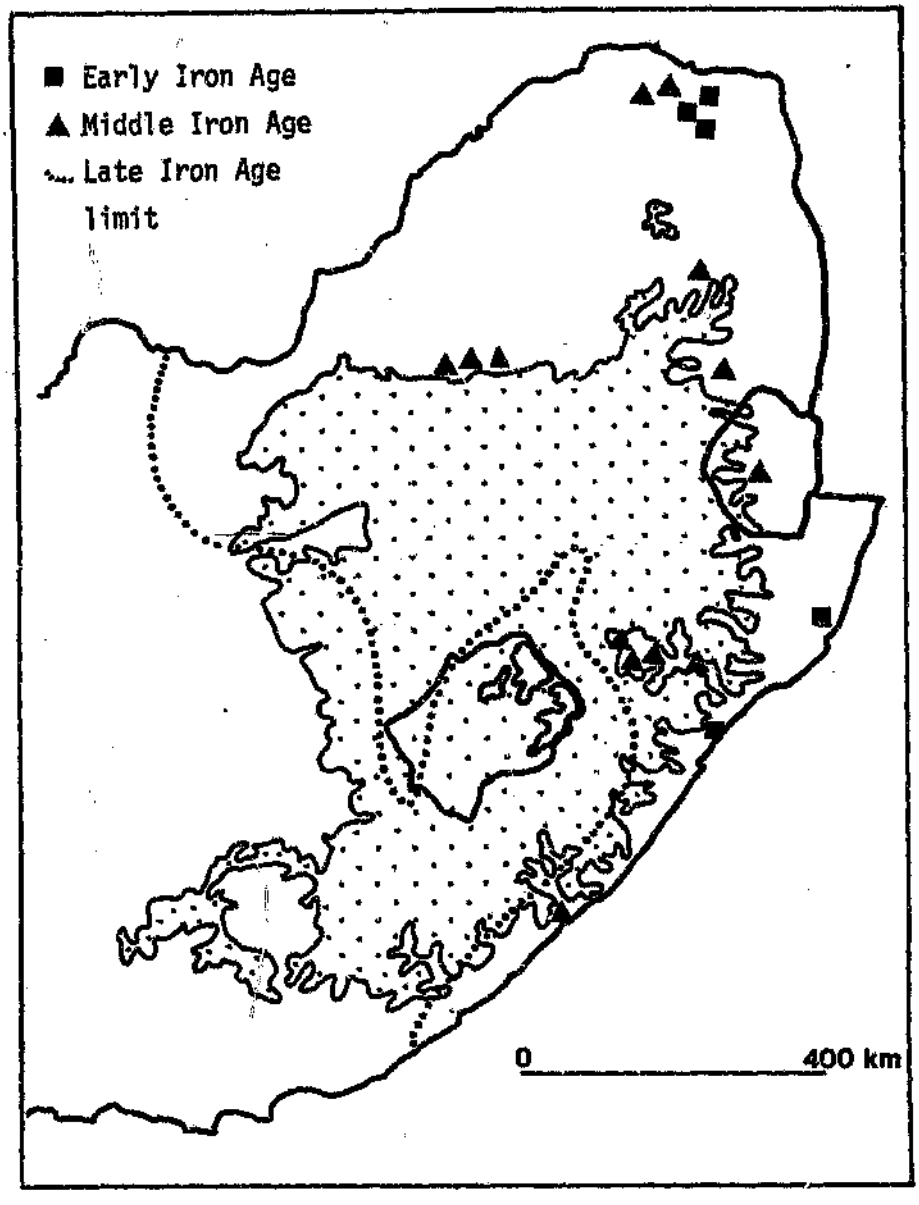


Figure 2.3: The distribution of Iron Age settlement sites in South Africa during the Early (up to approximately 500 AD), Middle (up to approximately 1000 AD) and Late (up to approximately 1700 AD) Iron Age periods, superimposed on a map of the grassland biome (stippled).

to areas north and east of the grassland biome as mapped by Rutherford & Westfall (1986). The movement of Late Iron Age people after this period into areas currently mapped as the grassland biome (Fig. 2.3) was accompanied by a number of adaptations indicative of a tree-less environment. Stone walling replaced the traditional use of wood for construction purposes, bone tools were used instead of iron tools, and dung was used as a major source of fuel (Maggs 1976, Hall & Maggs 1979). Furthermore, there are very few iron smelting sites in the area presently mapped as the grassland biome, presumably due to a shortage of wood. The increase in trade with people further north would have enabled the acquisition by people in the grasslands of iron tools and household utensils made of pottery. There is evidence of limited wood use for domestic purposes, and it would appear that the selection of sites within the grassland biome would have been for those that were wooded (Hall 1987). This may have resulted in the reduction of woody elements in what would appear to have been an essentially grassland habitat, but it seems unlikely that forest and savanna were converted to grassland by the activities of these people.

Further archaeological evidence is obtained in an examination of faunal skeleton remains obtained from Stone Age deposits in the grasslands in Natal, which Acocks (1975) considered seral to forest. Of the ungulates identified from these deposits, many of which are greater than 5 000 years old, the majority are associated with grasslands, (Cable et al. 1980, Maggs & Ward 1980, Klein 1984), including red hartebeest (Alcelaphus buselophus), black wildebeest (Connochaetes gnou), blesbuck (Damaliscus dorcas), quagga (Equus quagga), mountain zebra (Equus zebra), klipspringer (Oreotragus oreotragus), oribi (Ourebei ourebi), vaal rhebuck (Pelea capreolus), reedbuck (Redunca arundinum), mountain reedbuck (Redunca fulvorufula) and eland (Taurotragus oryx).

2.4.2.3 BIOGEOGRAPHICAL AND ECOLOGICAL EVIDENCE

The distributions of a number of faunal species in the grasslands considered by Acocks (1975) to be of recent origin, suggests a long evolutionary history (>>600 years). A number of typical grassland animals such as the redwing francolin (Francolinus levaillantii) have their distribution centred in the humid grasslands, and others such as the bald ibis (Geronticus calvus) are endemic (Siegfried 1971, Manry

1982, Tainton & Mentis 1984) to the same area. It seems incongruous that these animals have their distribution centred in an area which was forest or scrub forest just 600 years ago (Acocks 1975). The abundance and species richness of wildfowl, small mammals and antelope in the Natal Drakensberg are related to the time elapsed since the last fire (Mentis & Rowe-Rowe 1979). Faunal abundance and richness is greatest up to three years after fire and in areas never or rarely burned. Under an intermediate fire frequency, faunal abundance and richness are low. This bimodal distribution of faunal abundance and richness is unlikely if the biota of the fire accessible areas had not been exposed to fire for a great deal longer than the age that Acocks (1975) suggested as the age of these grasslands (Tainton & Mentis 1984).

Similarly, floral elements within the grassland biome indicate that the 'false' grasslands may be of great antiquity. The widespread distribution of Themeda triandra, a grass which has a very poor dispersal capability, in the grasslands of Natal, is not easily explained if the dominant vegetation in this area was forest or scrub-forest just 600 years ago (Mentis & Huntley 1982). Similarly, the flora of the grasslands in the areas suggested by Acocks (1975) to be seral to forest, scrub forest and savanna, is adapted to frequent defoliation by fire. Many grasses produce rhizomes or stolons at or close to the soil surface, and the tiller initials of these structures are stimulated by fire so that the plant is able to recover rapidly (Langer 1972, Tainton & Mentis 1984). Tufted perennial grasses appear better adapted to defoliation by fire than the sod-forming species (Tainton & Mentis 1984) and they occur over much of the biome, suggesting that frequent fire has long been a part of the grassland habit. The vernal aspect geophytes of the eastern grasslands depend on regular defoliation for their survival, in the absence of which they do not reach reproductive maturity and eventually die (Bayer 1955).

The present-day soils in areas of 'false' grassland also suggest that the area has been grassland for a great length of time. Some soils on the interfluves of the coastal hinterland of Natal have deep (up to greater than 1m) humic A-horizons (Mentis & Huntley 1982). In well drained upland sites, such depth of humified organic matter is thought to develop only under grass. Based on likely rates of pedogenesis the development of this horizon in a soil profile would take much longer than the few centuries proposed as the age of the 'false' grasslands.

2.4.3 IMPLICATIONS

The evidence indicates that the grassland biome as presently mapped has been in existence for millennia, and that the savannas and forests have been subject to much greater disturbance than the grasslands themselves (cf. Feely 1980). It may be that the boundaries of savannas, forests and grasslands have been modified from what they were prior to settlement by Iron Age people, but to invoke the biome-wide alteration of forest and savanna to grassland within the areas currently mapped as 'false' grasslands, over the last 5 or 6 centuries, is not supported by evidence from several disciplines.

This raises the question of the determinants of the distribution of the grassland biome, as it does not appear to have been the result of human activity in recent times as has often been suggested. Are the 'false' grasslands the result of human activity over a period much longer than the subcontinent has been inhabited by Iron Age people? Certainly it appears that fire has been a servant of humans in Africa for at least 100 000 years (Dimbleby 1977) and may have been used for 1 to 1.5 million (Brain & Sillen 1988). The existence of highly seasonal summer rainfall, and therefore of a prolonged dry season in the grasslands considered seral to forest or scrub-forest by Acocks (1975) and White (1983) may result in seasonal desiccation of the vegetation. In areas with a prolonged dry season it appears almost impossible to protect vegetation against man-made fires (Dimbleby 1977). The subcontinent has been inhabited by humans since our early evolution, and it is not unlikely that we have modified its vegetation by using fire (Hall 1984). Grasses have however been an important component of the vegetation for considerably longer than 50 million years (Stebbins 1974), and it is possible that natural fires have been responsible for the development of fire maintained grasslands prior to the time when humans could have initiated fires at will.

Alternatively, it has been argued by Rutherford & Westfall (1986), despite not being able to discriminate South Africa's grassland biome successfully using climatic indices, that climate is of overriding importance in determining its distribution. It has also been argued that the entire grassland biome may be edaphically determined (Feely 1987) rather than being maintained by either fire or climate.

It seems that in order to resolve the issue of the determinants of South Africa's grassland biome, generalised models are needed that provide some biologically meaningful insights into the historical and presently observed existence of grasslands in the regions in which they are presently mapped in southern Africa.

2.5 GRASSLAND FUNCTIONAL TYPES

The classification of the vegetation of South Africa including the grassland biome, and one which was explicitly based on the floristic characteristics as well as the practical utilization of vegetation for farming purposes, was the mapping of veld types by Acocks (1975). However, he used terminology in naming the veld types that was based on one or a combination of floristic, habitat and structural or functional attributes (Fig. 2.4). 'Cymbopogon-Themeda veld' is an example of a floristically based veld type name. Habitat features are embodied in terms such as 'mist belt', 'sandveld', 'coastal plateau' and 'turf veld', and structural or functional characteristics in terms such as 'sour', 'sweet', 'thorn' and 'tall'. Of the 27 veld types recognised in this study as comprising the grassland biome (cf. Table 2.2), the names given to 19 were based on criteria that have structural and/or functional significance, illustrating the perceived importance of structural and functional attributes at the time of Acocks's (1975) work. Little work has been done to follow up on the significance of Acocks's (1953) classification.

One of the most fundamental distinctions of Acocks (1975) that is of functional significance was based on differences in the seasonal pattern of forage quality. It formed the basis for the distinction of sweetveld, mixed veld and sourveld. Despite the importance of these vegetation types from the point of view of livestock production and range management, the distribution of these vegetation types, and their seasonal forage quality dynamics are poorly understood.

2.6 SUMMARY

The grassland biome is a distinct structural and functional unit at the subcontinental scale, based on the dominance of hemicryptophytes. Past and present views of the biome, and paradigms on which these views were based, have been examined.

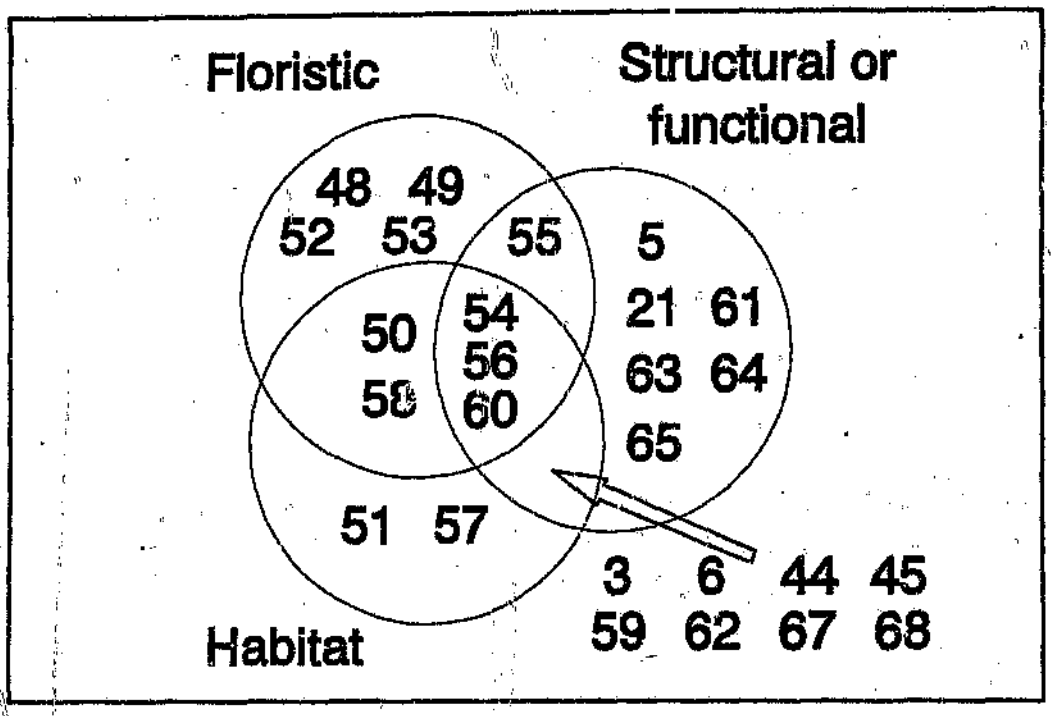


Figure 2.4: The veld type numbers included in the grassland biome in this study, that were named by Acocks (1975) using either or a combination of floristic, habitat and structural or functional terms. Refer to Table 2.2 for the names of the veld types for which numbers are given.

Recent information from a variety of disciplines suggests that the biome is of greater antiquity than previously thought, raising questions about the supposed anthropogenic origin of the 'false' grasslands east of the continental divide. This reopens the question about what determines the distribution of the biome as a whole.

At more detailed scales of resolution, past studies have proposed differences in grassland types based on species composition, habitat characteristics and structural and functional characteristics. The distinction between sweetveld, mixed veld and sourveld is important from the point of view of animal production and rangeland management within the grassland biome. However, their distribution and seasonal forage quality dynamics are poorly understood.

CHAPTER 3

BIOTIC AND ABIOTIC FEATURES OF THE GRASSLAND BIOME

3.1 INTRODUCTION

This chapter reviews literature on the geology, geomorphology, soils, climate, fire and fauna of the grassland biome. An overview of recent human impacts is also provided.

The grassland biome of South Africa covers an area of approximately 350 000 km^2 or 16.5% of the country (Rutherford & Westfall 1986). It occurs in the eastern half of the country, predominantly on the highveld, the Drakensberg escarpment and eastern seaboard hills (Fig. 3.1). Areas that are considered highveld include those areas of the eastern Cape, much of the Orange Free State and the southern and eastern Transvaal at an altitude between 1 000 and 1 800 m. Those areas of the Great Escarpment that comprise the Drakensberg are at altitudes above 1800 m, with much of the Lesotho Highlands above an altitude of 3300 m. The hills of the eastern seaboard include much of the eastern Cape, Transkei and Natal. They are deeply dissected, making up a belt up to 250 km wide discontinuously occupied by grassland.

The grassland biome is agriculturally the most productive region of South Africa, contributing overwhelmingly to the country's production of maize, dairy products, beef, mutton, wool and timber products (Mentis & Huntley 1982). In addition to this activity, much of the country's coal and mineral wealth is located within the grassland biome. This coincidence of agricultural, fossil fuel and mineral wealth makes it one of the most populous areas of South Africa, and the centre of industrialization and economic growth. The environmental repurcussions of these activities, as well as the potential of this area for resource deficiencies, are environmental problems that have been discussed by Mentis & Huntley (1982).

3.2 GEOLOGY AND GEOMORPHOLOGY

Salient aspects of the geological and geomorphological history of the region occupied

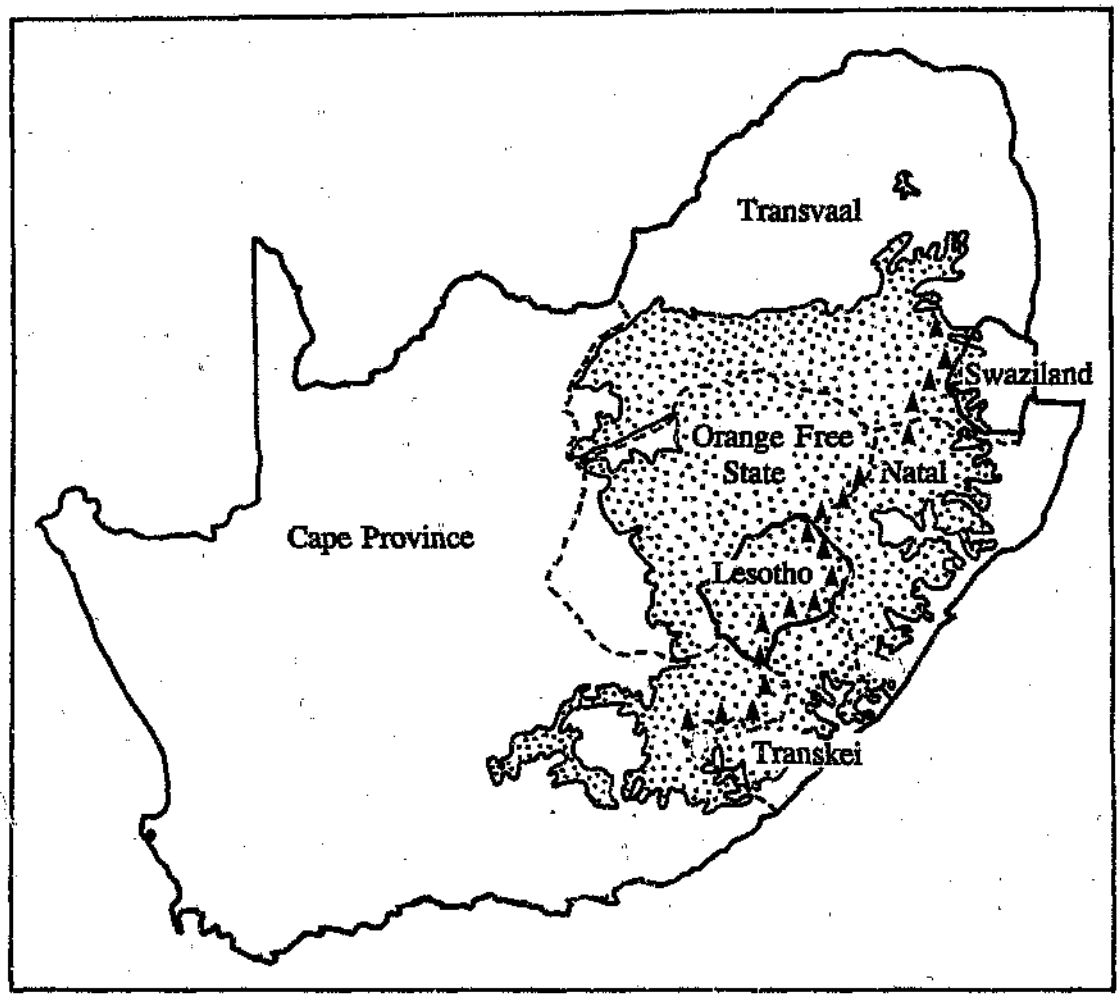


Figure 3.1: The distribution of the grassland biome (stipples) in South Africa. Province boundaries are indicated by dashed lines, and the Drakensberg escarpment by solid triangles.

by the grassland biome are described below. The information is drawn from Truswell (1977), King (1978), Tankard et al. (1982), Partridge & Maud (1987) and Moon & Dardis (1988).

The geological history of the subcontinent, summarised in Table 3.1 (after Tankard et al. 1982, Moon & Dardis 1988), extends back nearly 4 billion years. The early evolution of the subcontinent was associated with the formation of a stable granitic shield (craton) onto which there was extrusion of basic and ultrabasic lavas, and on which a number of sedimentary sequences were deposited (Truswell 1977). This makes up the Barberton Sequence, exposed in the eastern Transvaal in the region of Barberton and in Swaziland, with remnants exposed in the vicinity of Johannesburg (Halfway House Granite and its ultrabasic inclusions). Many of the exposed ultrabasics that form part of the Barberton Sequence are serpentinites which give rise to serpentine soils with endemic elements (Morrey et al. 1989).

This granitic basement and its volcanic and sedimentary inclusions were buried in a series of depositional basins that developed from 3.0 to 1.75 billion years BP. These include the Pongola Sequence, the Witwatersrand and Ventersdorp Supergroups and the Transvaal and Griqualand West Sequences. Further discussion of each of these units will be confined to areas where they are exposed within the grassland biome (Fig. 3.2). The Griqualand West sequence is not exposed at all in the grassland biome. The Pongola Sequence, which is exposed in Swaziland and northern Natal, comprises an alternating sequence of quartzites and basalts, with shales forming a minor component (Truswell 1977). The Witwatersrand Supergroup is a thick sequence of shales, quartzites and conglomerates, with minor volcanics and banded ironstones. Exposure is restricted to the Witwatersrand, Heidelberg, Vredefort and north-east of Klerksdorp in the south-western Transvaal. The Ventersdorp Supergroup is a mass of predominantly volcanic rocks, primarily andesitic lavas, which is exposed in the southern and western Transvaal. The Transvaal Sequence is exposed in the western, southern and eastern Transvaal, being of volcanic and sedimentary sequences. The sedimentary sequences include a lower quartzite, above which is a thick dolomite sequence. Above these is a sequence of quartzites, shales and volcanics.

Geomorphic events elsewhere on the subcontinent include the deposition of the

TABLE 3.1: Stages in the geological development of southern Africa (after Tankard et al. 1982, Moon & Dardis 1988). Ages are in millions of years (Ma), and sequences that are not present in the grassland biome are recorded in brackets.

AGE (Ma)	MAJOR GEOMORPHIC EVENTS
0	Recent deposits
	Karoo volcanics
	Karoo Sequence
	(Cape folding)
500	Cape Supergroup
1000	Metamorphism and granitic intrusion
1500	
	(Waterberg Group)
2000	(Bushveld Complex)
	Transvaal (and Griqualand West) Sequences
2500	
	Ventersdorp Supergroup
	Witwatersrand Supergroup
	Pongola Sequence
3000	
3500	Granitic crustal development
4000	

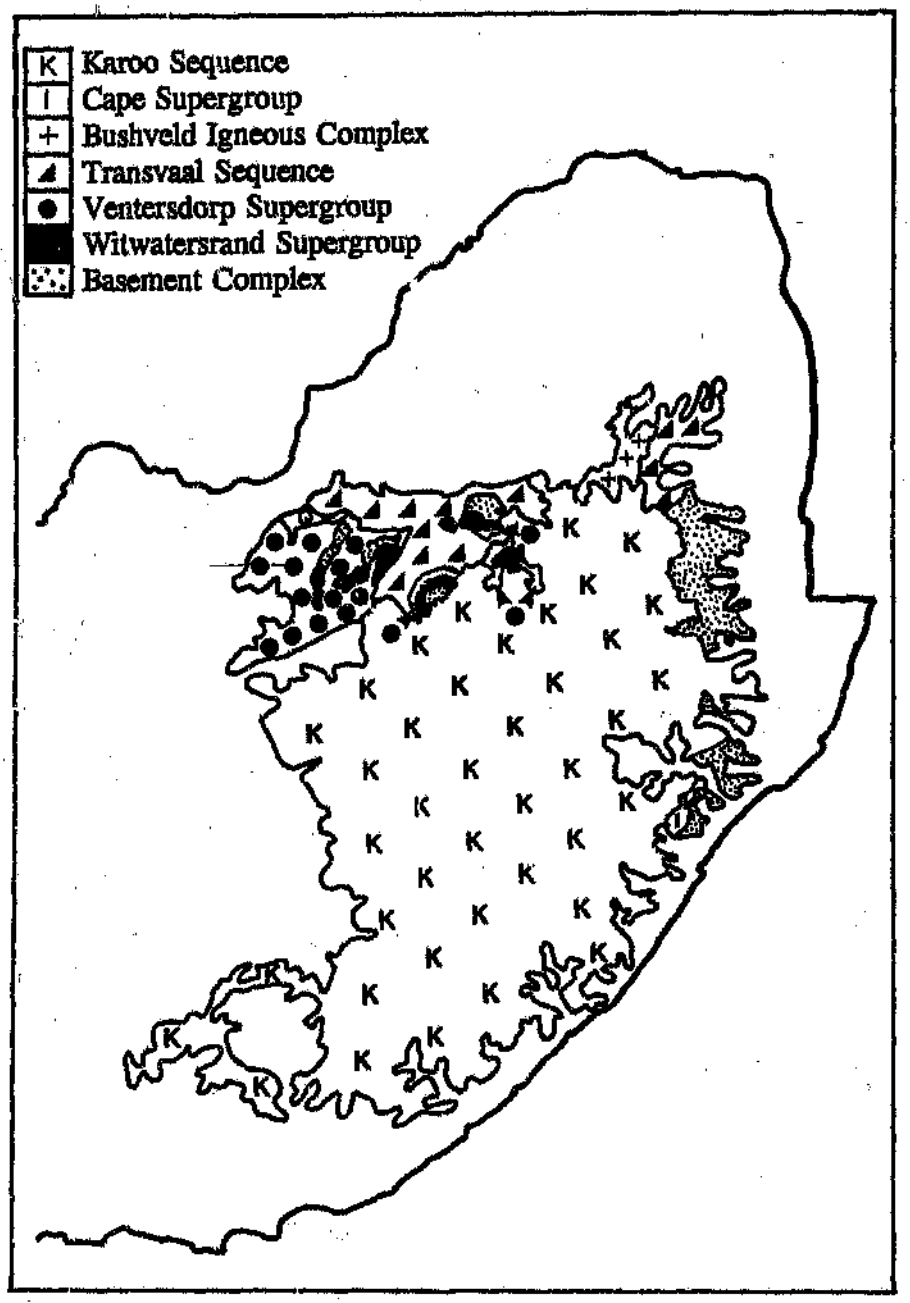


Figure 3.2: The distribution of major geological units (after Truswell 1977) superimposed on a map of the grassland biome.

Waterberg Group, and emplacement of the Bushveld Igneous Complex onto the rocks of the Transvaal Sequence. This was followed by a phase of tectonic activity, metamorphism, and intrusion of granitoid rocks from the mantle, which covered the period from 1.75 to approximately 0.5 billion (500 million) years BP.

At this time Africa lay at the centre of Gondwanaland. Rocks of the Cape Supergroup were deposited from approximately 500 to 400 million years BP, composed of orthoquartzites, sandstones, siltstones and shales. These rocks are exposed in the south-western and southern Cape, as well as in much of Natal, and can be matched with rocks in South America, the Falkland Islands and Antarctica (Truswell 1977). These strata are covered by rocks of the Karoo Sequence that range in age from approximately 300 to 160 million years BP. These rocks cover much of South Africa, including by far the greater part of the grassland biome. They are primarily composed of sediments of the Ecca and Beaufort Groups, and the Molteno, Elliot and Clarens Formations. Sandstones, mudstones and shales predominate throughout. The Karoo system is associated with a rich fossil flora and fauna which are matched in other southern continents.

The final phase of the geological evolution of southern Africa was associated with the break-up of Gondwanaland, with massive extrusion of basalt onto the existing land surface. Much of this is exposed in the highlands in Lesotho, and in the high Drakensberg north and south of Lesotho. Associated with this extrusion was the intrusion of existing strata by dolerites, which are exposed throughout the grassland biome. The vulcanicity that terminated the Karoo sequence was active until approximately 120 million years BP.

The fragmentation of Gondwanaland was associated wi significant downwarping of the continental margins, a feature that gave rise to the Natal monocline (King 1982). However, an elevated zone developed parallel to the continental margin, reflecting uplift associated with rifting and continental fragmentation. This series of events gave rise to the presently observed macro-scale topographic configuration of southern Africa, with a central depression bounded by higher land and an abrupt outward facing escarpment. The Great Escarpment which seperates the interior plateau from the coastal regions, was initiated by erosion on the downwarped margins to the base

level afforded by the newly formed coastline (Ollier & Marker 1985).

Since the break-up of Gondwanaland, Africa has been erosional. The broad-scale geomorphic evolution of the subcontinent has been the result of periods of tectonic uplift since then. Each period of uplift has caused erosion to new base levels (Table 3.2). The African erosional phase appears to have lasted for more than 100 million years, from the opening of the ocean basins associated with the breakup of Gondwanaland (approx. 140 million years BP) to the Miocene (approx. 18 million years BP). This major period of landscape development ended with uplift during the Miocene, which initiated the Post African I erosional phase. This phase of landscape development ended with uplift in the Pliocene, approximately 2,5 million years BP, at which time Post-Africa II erosion was initiated.

The most recent interpretation of the geomorphic evolution of southern Africa is that of Partridge & Maud (1987). Based on this the grassland biome can be divided geomorphologically into four major regions (Fig. 3.3). Firstly, the highlands above the African land surface represent the most ancient land surfaces that predate and immediately follow the formation of the African continent. Secondly, the Great Escarpment Zone is distinguished from these highlands. Thirdly, the belt east of the Great Escarpment, which includes much of the Natal monocline, is a dissected area with major structural control. Some of the interfluves represent areas where the African land surface has been preserved, but generally they represent the Post-African surface. Fourthly, to the west of the Great Escarpment and highlands, the highveld consists of a gently rolling landsurface in which the Post-African surface is partly planed.

3.3 SOILS

The soils of southern Africa have not been described in any great detail at the subcontinental scale, with Harmse's (1978) schematic soil map being the most useful for the purposes of the present description. This scheme reflects genetic factors of soil formation with an emphasis on features that are relevant to the distribution of natural vegetation.

TABLE 3.2: Stages in the geomorphological development of southern Africa (simplified after Partridge & Maud 1987, Moon & Dardis 1988). Ages are given in millions of years (Ma). Tectonic events that set new base levels and therefore control the development of erosional surfaces are set against the left margin in column 2, while the resulting erosional surfaces are indented and shown in bold.

AGE (Ma)	MAJOR GEOMORPHOLOGICAL EVENT
0	**Post African II erosion**
	Major uplift (approx. 2,5 Ma)
	Post African I erosion
	Moderate uplift (approx. 18 Ma)
50	
	African erosion
100	
	Formation of western and southern coastlines (late Gondwanaland fragmentation)
	Formation of eastern coastline (initial fragmentation of Gondwanaland)
150	

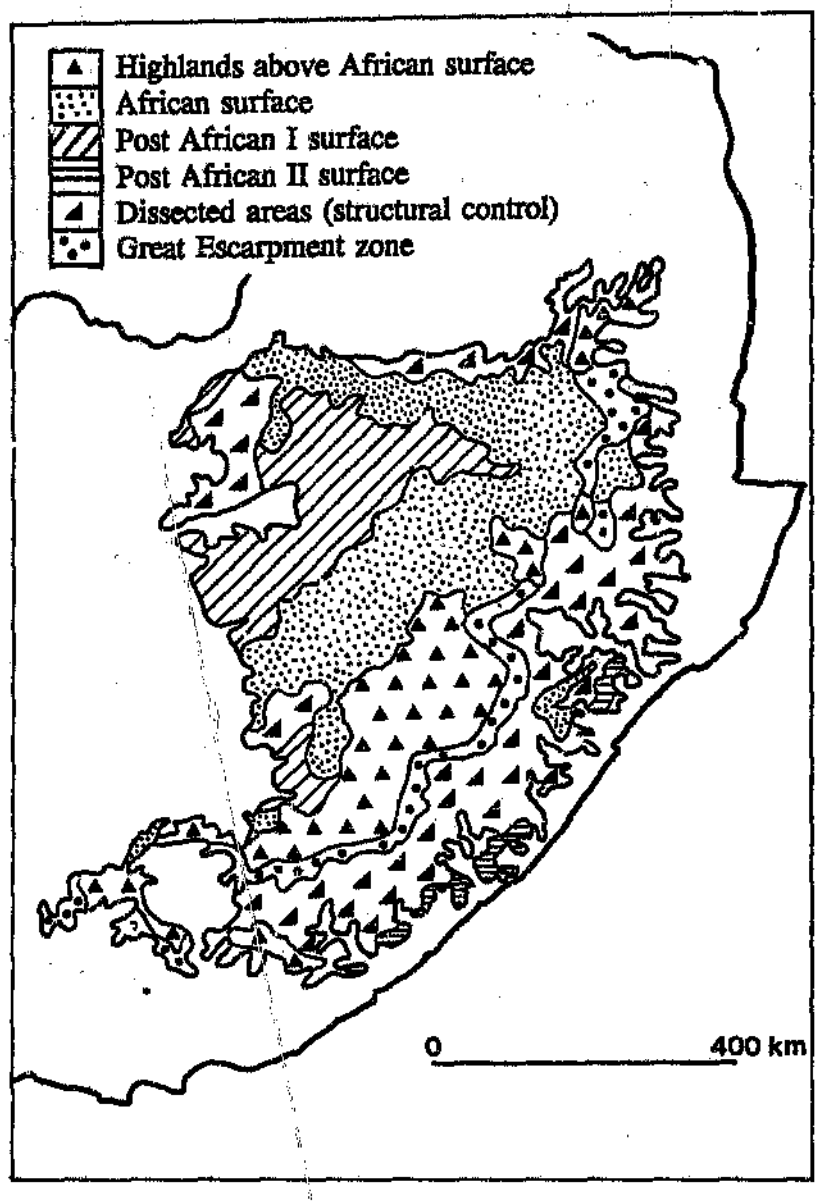


Figure 3.3: The distribution of major erosion surfaces and dissected areas (simplified after Partridge & Maud 1987; Moon & Dardis 1988) superimposed on a map of the grassland biome.

Much of the region of the country with high rainfall (including the eastern seaboard and its interior, as well as the escarpment of the eastern Transvaal), comprises ferrallitic soils with weakly differentiated horizons. These soils have little remaining weatherable material, and the clay minerals are of the 1:1 lattice type mixed with significant quantities of free iron oxides and occasionally aluminium oxides. The cation exchange capacity, as well as the degree of base saturation of these soils, is usually low.

The highlands above the African erosion surface (including those in Lesotho and in the eastern Transvaal) are primarily lithosols. These shallow soils show weak profile differentiation, and contain coarse fragments of solid rock at a relatively shallow depth within the soil profile (usually less than 0.5 m).

Soils of dissected areas of the eastern seaboard are sometimes derived from basic or even ultrabasic volcanic rocks, giving rise to dark coloured montmorillinitic clay soils. They tend to predominate in warm, dry, inland lowland areas of Natal as well as in the eastern Cape. These soil types also occur on the highveld in the south-eastern Transvaal, where dolerite forms the parent material.

In areas of intermediate rainfall (including north-western Natal, the eastern Orange Free State, and the southern, south-western and eastern Transvaal highveld), fersiallitic soils are predominant. These have diffuse transitions between horizons and weakly to moderately developed structure in the B-horizons. The reserve of weatherable material is variable, depending on the parent material, as is the amount of 2:1 lattice clay. Kaolinite is generally the dominant clay mineral.

Soils of the remainder of the biome (central and north-eastern Orange Free State and the eastern Cape) are classified as solonetzic and planosolic soils. These soils have moderately to strongly developed pedocutanic or prismacutanic B-horizons. Sometimes these are enriched in sodium or magnesium.

Aspects of soil fertility have been described by Mentis & Huntley (1982). In areas of the Lesotho Highlands above the African erosion surface, erosion is extreme. Soils are skeletal due to steep slopes, and low temperatures which limit weathering

processes. Where the pre-African erosion surface is still intact, soils may be dystrophic (Mentis & Huntley 1982). Those of the monoclinal region tend to be heterogeneous because of localised differences in topography and parent material. The low-lying land surfaces in the interior regions of the monoclinal region are relatively young, warm and dry, and therefore tend to be eutrophic. In contrast, the soils of the interfluves at higher elevation in this region tend to be leached due to their occurrence on more ancient land surfaces and in areas with high rainfall. The highveld also has heterogeneous soils. Soils in the semi-arid areas in the west are eutrophic due to low levels of weathering and leaching. Eastwards, precipitation increases, and so too does weathering and leaching. Eutrophic, black 'turf'[1] soils derived from basic igneous rocks, particularly dolerite, occur as pockets in these otherwise dystrophic highveld soils.

3.4 CLIMATE

The main features of climate of the grassland biome are described by Schulze & McGee (1978), who recognise that radiation, temperature and moisture are the major climatic determinants of vegetation development.

3.4.1 SOLAR RADIATION

Solar radiation is the most fundamental of all climatic parameters, providing the major energy source for all ecosystems. Altitude, sunshine duration, atmospheric water content, cloud cover and atmospheric dust content are all recognised to affect the amount of solar radiation striking the earth's surface. During winter there is an increase in solar radiation from the south-east of the subcontinent to the north-west, with mean values of 11 x 10^6 $J.m^{-2}.day^{-1}$ along the southern coast, to 16 x 10^6 $J.m^{-2}.day^{-1}$ in the northern Cape and north-western Transvaal. These values are applicable from south to north in the grassland biome. During summer there is an increase in solar radiation from east to west across the subcontinent, with minimum mean values of 21 x 10^6 $J.m^{-2}.day^{-1}$ along the coast of Natal and Transkei, and maximum values

[1] 'Turf' refers to dark coloured clayey soils with shrink-swell properties, technically vertisols.

of 30 x 10^6 J.m^{-2}.day^{-1} in the far north-western Cape. This largely reflects patterns of cloud cover. The grassland biome experiences values from 21 to 26 x 10^6 J.m^{-2}.day^{-1} at this time of the year.

3.4.2 TEMPERATURE

Critical temperature indices such as summer mean daily maximum and winter mean daily minimum temperatures are considered more important than mean monthly or mean annual values, in their affects on the distribution of major regional vegetation formations (Rutherford & Westfall 1986). Mean annual temperatures of the grassland biome vary from 14°C to 20°C. These values are similar to those over the entire subcontinent. The mean daily maximum temperatures in January in the grassland biome vary from 25°C to 30°C, which is lower than the daily maximum January temperatures in the arid and semi-arid areas in the interior, but higher than temperatures along the southern and western coastal areas, where cool ocean temperatures moderate the daily maximum temperatures. The mean daily minimum temperatures in July in the grassland biome are amongst the lowest in the country, with values of -2,5°C in the region of the Great Escarpment. Much of the grassland biome of the highveld experiences mean daily minimum temperatures lower than 0°C in July. East of the continental divide values rise steadily eastwards to approximately 10°C along the east coast. The mean daily temperatures in the grassland biome both in January and July are cooler than in other areas of the subcontinent.

3.4.3 MOISTURE AVAILABILITY

Rainfall is the major form of precipitation. It occurs in summer, and increases from approximately 400mm in the west to about 1000mm in the east of the biome. Superimposed on this general pattern, the effects of topography give rise to local differences, with up to 1800mm on the slopes of the Natal Drakensberg and less than 600mm in parts of the Natal midlands such as the Tugela basin east of the Drakensberg. A marginal (less than 100mm) to moderate (200-400mm) average water surplus is experienced during the period December to April, with deficiencies in the remaining months (Mentis & Huntley 1982).

3.5 FIRE

Fire is an extremely important abiotic factor in the grassland biome. Both natural and anthropogenic fires have undoubtedly occurred widely and relatively frequently for many millenia in the grassland biome (Hall 1984), and they have had an important influence in shaping the grasslands as they are presently known (Tainton & Mentis 1984). Burning has received considerable attention from researchers in southern Africa for over 70 years, and continues to receive great emphasis, particularly its effect on species composition, cover, yield, forage quality, shrub encroachment, faunal structure and soil properties including water yield. There is a wealth of literature on the role of fire in South Africa's grasslands (Tainton 1984), with a comprehensive review by Tainton & Mentis (1984). Three key issues are considered relevant for the present study. Firstly, the effect of fire on vegetation structure is pertinent to aspects related to the distribution of woody plants at the biome-wide and landscape scale. Within the moist grasslands, fire is considered responsible for the grassland habit, recurrent fire favouring grasses at the expense of woody plants. In the absence of fire, succession is considered to result in the establishment of wooded communities (Killick 1963, Mentis et al. 1974, Acocks 1975, Tainton 1981, Tainton & Mentis 1984). Fire is therefore an important aspect of rangeland management in the moist grasslands, and is used to remove excess litter accumulation as well as to prevent the establishment of woody plants (Tainton & Mentis 1984). The highveld grasslands however, are considered the climax community, and in the absence of fire are considered to retain the grassland habit (Acocks 1975, Tainton 1981, Tainton & Mentis 1984).

Secondly, the effect of burning on herbage production and forage quality is pertinent to the classification of different grassland types within the grassland biome, with fire regimes and their effects differing fundamentally in the 'sweet' and 'sour' grassland types. In the moist sour grasslands, where primary production is high (Rutherford 1978), foliage becomes progressively less acceptable to grazers as it matures. By the end of the growing season it is unpalatable, and large quantities of unused foliage remain intact. The combination of increased production and decreased acceptability to grazers results in the accumulation of large quantities of dead standing grass in sourveld areas. This eventually shades out the dominant perennial grasses, which

gradually die off (Stuart-Hill & Mentis 1982, Tainton & Mentis 1984). Under light grazing, frequent fire therefore stimulates production in the sourveld areas, and it also improves forage quality (Mes 1958, Downing et al. 1978, Tainton & Mentis 1984). The sweet grasslands experience lower rainfall, and herbage production is correspondingly lower than in the sour grasslands. Forage quality however remains relatively high throughout the year, and grazers tend to consume standing grass leaf material. At appropriate stocking rates it is therefore not necessary, or even possible, to burn in these areas (du Toit 1972, Tainton 1981, Mentis & Huntley 1982, Stuart-Hill & Mentis 1982).

Thirdly, the effect of fire on edaphic conditions and microclimate, particularly nutrient availability, moisture availability and temperature are important. A number of soil physical and chemical properties are altered by burning. The literature is somewhat contradictory, with much variation in the observed results reflecting the range of potential fire effects. Nitrogen and phosphorus are the nutrients frequently most limiting to plant communities in natural ecosystems (Chapin 1980), and will be emphasised here. Much of the nitrogen contained in the above-ground standing crop is gasified during burning, but where combustion is incomplete, some organic nitrogen is returned to the soil surface as residue (DeBell & Ralston 1970, Christensen 1977, Raison 1979, Christensen 1987). Reports of the amounts lost by volatilization as a proportion of the total standing crop vary considerably, being higher in light fuels such as grasses, and for any particular fuel, at higher temperatures (DeBell & Ralston 1970, Raison 1979). White & Grossman (1972) showed that annual burning in a highveld grassland reduced the concentration of nitrogen in the soil from 0,066% to 0,059% over a period of 37 years. Losses to volatilization of other nutrients appear to be less than those for nitrogen, but nevertheless may result in a decline in the total available pool, as indicated for calcium, magnesium, potassium and sodium concentration in the same experiment (White & Grossman 1972). The phosphorus concentration in the soil of sites burned annually did not differ from unburned sites. The long-term consequences of burning for total nutrient capital have not been thoroughly studied in the grasslands of South Africa, despite its apparent importance.

Although fire may cause an overall loss in nutrient capital, it can result in increased

concentration of available nutrients. This may occur directly as a result of mineralization during a fire and the addition of mineralized material to the soil surface, or it may occur indirectly by altering soil moisture or temperature, or by altering ion exchange properties, thereby affecting microbial activity. Although no data are available for the grassland biome in South Africa, data from grasslands elsewhere in the world suggest that fire increases nutrient availability in the short term (Vogl 1974, Stock & Lewis 1986, Hulbert 1988).

The effect of fire on microclimate has been reasonably well studied in the grassland biome (cf. Tainton & Mentis 1984). Surface daytime temperatures increase substantially, while those at night decrease on burned veld compared to unburned veld (Phillips 1919, 1930, Mentis & Bigalke 1979, Savage 1980). This should stimulate growth (provided moisture is available) in early spring following late winter or early spring burning, a time when temperatures may limit growth and soil microbial activity. Clearly the overall effect is dependant on the time of year of the burn (Tainton & Mentis 1984). The effect of fire on the moisture balance is complex, and generalizations are difficult. Burning may reduce interception by the canopy and increase the effectiveness of small rainfall events, or it may reduce or increase runoff (depending on the architecture of the canopy) by concentrating rainfall onto or between tufts respectively (Glover et al. 1962, Tainton & Mentis 1984). Tainton & Mentis (1984) present data showing increased infiltration potential of soils less frequently burned. Burned grasslands lose greater quantities of moisture by evapotranspiration, both by increased evaporation from the soil surface due to increased temperatures, and by increased transpiration because of increased productivity of the sward. Despite the contradictory results obtained for moisture relations on burned sites compared to unburned sites, there is general feeling that soils dry out more rapidly following burning (Tainton & Mentis 1984).

3.6 FAUNA

In former times it seems that a rich ungulate fauna occurred in the grassland biome, including black wildebeest, blesbok, red hartebeest and springbok (Mentis & Huntley 1982), but overexploitation caused the virtual extinction of these animals. Between 1870 and 1880 nearly 2 million 'buck skins' passed through Durban harbour, and by

1890 they ceased to be of economic significance (Mentis & Huntley 1982). In addition to these migratory ungulates, resident animals included grey rhebuck, common reedbuck, mountain reedbuck and oribi.

Today, domestic animal production in the grassland biome is of great economic significance. It includes dairy, beef and wool production, with carrying capacities between 5 ha.LSU^{-1} in the more arid areas and 1,75 ha.LSU^{-1} in the moist grasslands [2] (Tainton 1981). Animal production relies largely on natural pasture (Tainton et al. 1989), although planted pastures are reasonably widespread in the moist grasslands of Natal (Booysen 1981).

The grassland avifauna includes some 21 endemic species, of which a number are threatened, rare or endangered, including the bald ibis, crowned crane, blue korhaan, ground woodpecker, Botha's lark, Rudd's lark and the blue swallow.

3.7 HUMAN IMPACT

Although the grassland biome has been inhabited by Stone Age people for many tens of thousands of years, these people are considered to have had a negligible impact in the environment. Iron Age people and European settlers, who have inhabited the grassland biome for less than 1000 years and less than 200 years respectively, have left a clearer mark. Despite being the most recently inhabited biome by Iron Age people and European settlers, the grassland biome today is the most populous in southern Africa. This is largely attributable to the presence of major economic reserves of gold and coal within the biome.

The importance of the grassland biome for animal production has been alluded to previously. Cultivation of crops is also important. The production area for the southern African staple crop, maize, is centered in the grassland biome. Other important crops are sorghum, wheat and sunflowers. Silviculture is also widespread in the grassland biome, with timber and paper the major products.

---

[2] The Large Stock Unit (LSU) is defined as a steer of 450 kg mass, gaining 500 g mass per day on a grass pasture with a mean digestible energy content of 55% (Meissner 1983).

The environmental problems within the grassland biome relate largely to human needs and impacts. Population growth in South Africa, and particularly the growth of the urban population in the region of the Pretoria-Witwatersrand complex, is likely to lead to environmental problems (Jordaan 1991). Arable land is a scarce resource in South Africa, with much of it already cultivated. Losses to urbanization and industrialization are not likely to be compensated for by ploughing new areas (Mentis & Huntley 1982). A second resource which is scarce is water. Projected needs for the Pretoria-Witwatersrand complex alone indicate massive deficits if the water is supplied locally, with multinational inter-basin transfer of water under way to meet this shortfall.

Soil loss and rangeland degradation are aspects of resource depletion that are of major concern in the grassland biome (Mentis & Huntley 1982). Soil losses tend to be greatest in areas presently most intensively utilized for agricultural production. Rangeland degradation of the grassland biome has been discussed at length, with invasion of grassland by karoo and by thornveld considered a consequence of poor rangeland management over the past 300 years (Acocks 1975, Acocks 1964, Roux & Vorster 1983, Roux & Theron 1987, Hoffman & Cowling 1990). Invasion of grassland by karoo was considered to have been 'the most spectacular of all the changes in the vegetation of South Africa' (Acocks 1975). This claim will be examined later in the study.

3.8 SUMMARY

The geology, geomorphology, soils, climate, natural disturbance (fire and grazing), and human impacts of the grassland biome have been reviewed, with an emphasis on features that are likely to affect vegetation. Geologically, the region is diverse, with parent materials varying in age and composition. Parent material comprises ultrabasic volcanic rocks such as serpentine, basic volcanic rocks such as basalt and diorite, rocks of intermediate base status such as granites, shales and mudstones, and acidic rocks such as sandstones and quartzites. Geomorphologically, erosional surfaces can be recognised that are associated with periods of uplift during and after the breakup of Gondwanaland, and the grassland biome can be divided into four regions; the highlands above the African erosional surface, the Great Escarpment, the Natal

Monocline and the highveld. Soils are also variable, generally being related to parent material, geomorphology, and climate. Soil fertility is also described in a general way. The climate of the biome is characterised by summer rainfall which increases from west to east, with temperatures increasing from east to west. Winter temperatures are lower in the grassland biome than in any other biome in South Africa. Fire is an important feature of the grassland biome, and its effects on vegetation structure, herbage production and forage quality, and nutrient availability are discussed. Historically, the grassland biome appears to have supported a diverse ungulate fauna, but this has been reduced by past overexploitation. Presently the grassland biome is important from the point of view of commercial animal production. The mineral wealth and agricultural potential in much of the grassland biome has resulted in it containing the most densely populated centres in the subcontinent, a feature likely to lead to environmental degradation and increasing shortages of natural resources such as water and arable land.

CHAPTER 4

DEVELOPING PREDICTIVE UNDERSTANDING OF THE DETERMINANTS OF THE GRASSLAND BIOME

4.1 INTRODUCTION

The distribution of the grassland biome as it is presently mapped in South Africa, is poorly understood, with one or a combination of climate, fire and soils having been suggested as important. The 'pure' (climatically determined) and 'false' (anthropogenically induced, fire maintained) dichotomy is not well founded. The presence of soils considered to determine the distribution of the grassland biome (those with a 'well developed cutanic B-horizon'; Feely 1987) in biomes other than the grassland biome, suggests that something other than soils is important. Past attempts to discriminate the grassland biome based on climate alone are weak. The objective of this section of the study was to determine whether the distribution of the grassland biome of South Africa can be related to climate, and if so, to identify important features of its climate.

The co-incidence of boundaries of natural vegetation zones and climatic regions has generally been held to illustrate the importance of climate as a determinant of vegetation distribution at a global, continental or subcontinental scale. The relationship between climate and plant distribution is generally described empirically by correlations between various macro-climatic variables and different vegetation units (Fitzpatrick & Nix 1970, Sowell 1985, Rutherford & Westfall 1986, Stephenson 1990). Recent studies have focussed on determining particular aspects of climate that most influence the distribution of vegetation types, and by what mechanisms. The most useful climatic parameters involve both energy supply (temperature, radiation, potential evapotranspiration), water supply (precipitation), and interactions between the two (actual evapotranspiration; Thornthwaite 1948, Holdridge 1967, Mather & Yoshioka 1968, Budyko 1974, Whittaker 1975, Woodward 1987, Stephenson 1990).

The most comprehensive attempt to discriminate the biomes of southern Africa based on climatic indices was by Rutherford & Westfall (1986). Their categorization of

South Africa's biomes was based on four indices. These were the rainfall during the four warmest months of the year, the proportion of the total rainfall during the six winter months, rainfall during the six summer months, and the mean minimum temperature of the coldest month. By their own admission, discrimination of the grassland biome was poor. Shortcomings of their model may have been due to failure of the assumption, as suggested by Bond & Richardson (1990), that climate is the overriding determinant of vegetation distribution - even at a biome-wide scale. Alternatively, their choice of indices may have had little biological significance. The choice by Rutherford & Westfall (1986) of using rainfall during the summer and winter half-year periods as indices of plant available moisture, involved the somewhat arbitrary choice of summer as the six-month period from October to March and winter as the period April to September. Similarly, their use of a 'summer aridity index', although less arbitrary than the previous two indices, focuses on rainfall during a fixed four month period.

Techniques are available to give more biologically meaningful measures of water and energy supply than simply using rainfall data or potential evapotranspiration. Use of a water balance approach has been shown to be of great value (Stephenson 1990). The emphasis in this component of the study is on the development of biologically meaningful climatic indices that can be related to South Africa's biomes, with an emphasis on the grassland biome. The approach adopted in this study is similar to that of Stephenson (1990), with the exception that daily records are used in this study, and the output of the present exercise is in units that are biologically intuitive.

4.2 METHODS

4.2.1 SELECTION OF CLIMATIC INDICES BASED ON OTHER STUDIES

A wide range of climatic indices were used in the present study, including many that have been used in similar studies in southern Africa and elsewhere. Indices used in other studies are described in this section. Those unique to this study are described in the following section (4.2.2).

Values for climatic indices were calculated for 163 weather stations (Fig. 4.1) in the

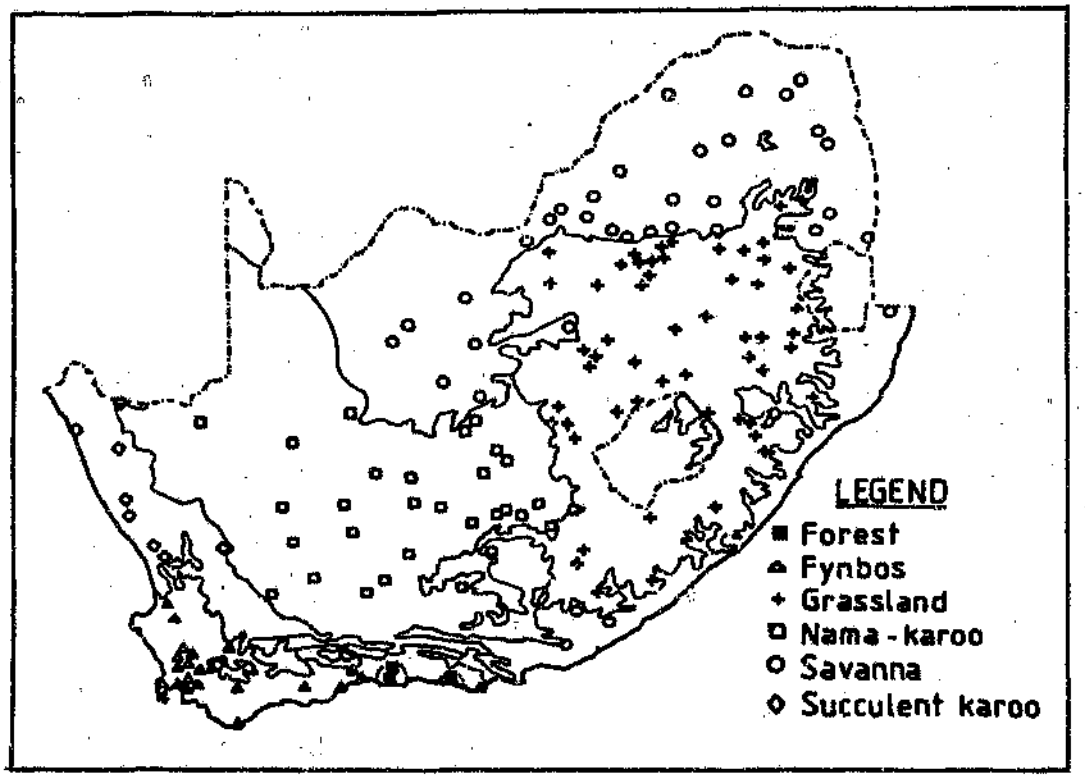


Figure 4.1: The distribution of weather stations used in this study to discriminate South Africa's biomes (after Rutherford & Westfall 1986) on the basis of climatic indices.

biome types described by Rutherford & Westfall (1986). These indices were calculated from records of the Weather Bureau (1988), with greater than 20 years of data. This minimum duration was chosen due to the possible presence of rainfall cycles with a periodicity of approximately 20 years (Tyson 1987). The indices used were mean annual rainfall (RAIN), mean summer half-year rainfall (October to March; SHYR), proportion of rainfall in the winter half-year period (April to September; RWINT), summer aridity index (SAI; using the method of Rutherford & Westfall 1986), mean annual temperature (ANTEM), and the mean minimum temperature for the coldest month (MMT).

4.2.2 USE OF INDICES DERIVED FROM THE WATER BUDGET MODEL

Confusion that exists in the terminology related to water balance parameters has been highlighted by Stephenson (1990). In order to avoid confusion in this study, terms are defined briefly. They follow Ayoade (1988) and Stephenson (1990).

Potential evaporation is an index of total energy supply in the environment, being an estimate of evaporation from a large, deep, open water body which exerts negligible resistance to water transport away from the surface.

Potential evapotranspiration is related to the amount of biologically usable energy in the environment, being the evaporative water loss from a site covered by a standard crop that is independant of the particular vegetation at a site. Generally, the standard crop is a continuous sward of short green grass that completely shades the soil surface, is not limited by nutrients or water, and exerts negligible resistance to water movement.

Precipitation is the amount of liquid that falls to the ground over a given period. It is assumed to be the water supply in most studies (including this study). A problem with this assumption is that where precipitation falls in solid form, it may be available as water supply at a different time of the year to that at which it is recorded as precipitation. The relatively small quantity of annual precipitation in South Africa as snow or ice makes this assumption acceptable. A further problem with this assumption is that it does not take into account runoff, runon or lateral seepage.

Actual evaporation is a measure of the simultaneous availability of total energy and water supply. It is the evaporative water loss given the prevailing water supply, and equals whichever is the least of water supply or potential evaporation.

In recognition of the advantages of a water balance approach, the moisture and temperature regimes of the same 163 weather stations described in the previous section were calculated using a water balance model summarised in Fig. 4.2. The mean number of days per annum on which sufficient water is available to permit plant growth was considered a biologically meaningful index of water availability. This number, called 'growth days' (GDAYS), was calculated using the water balance model based on daily rainfall and daily potential evaporation, giving a measure that is equivalent to actual evaporation. Actual evaporation was used as the index of simultaneous energy and water availability in this study, so that plants that occur at a site did not have to be stipulated *a priori*. Since maximum evaporation from a vegetated surface under non-advecting conditions is typically between 50% and 80% of actual evaporation due to the additional resistance imposed by the canopy, this assumption means that the actual duration of the growing season will be greater than the number of growth days calculated using actual evaporation.

To ensure consistency between stations, which had rainfall records of variable length and quality, daily rainfall sequences were generated for 100 years for each station using the rainfall simulation model (Zucchini & Adamson 1984, Zucchini et al. 1992). Linacre's (1977) procedure for calculating monthly potential evaporation requires as input altitude, latitude, and mean monthly maximum and minimum temperatures. These data were obtained from records of the Weather Bureau (1988).

The model calculates 'growth days' on the basis of sufficient water being present in the soil reservoir to completely satisfy potential evaporation. In reality, plant growth does not end abruptly as the soil dries out, but tapers off over a period of days. This is another reason why 'growth days' will be shorter than the observed growing period in the field, but it should correlate well with plant productivity, since plant production is proportional to to actual evaporation (Rosenzweig 1968, Stephenson 1990).

The mean temperature on days when water was available for growth was recorded as

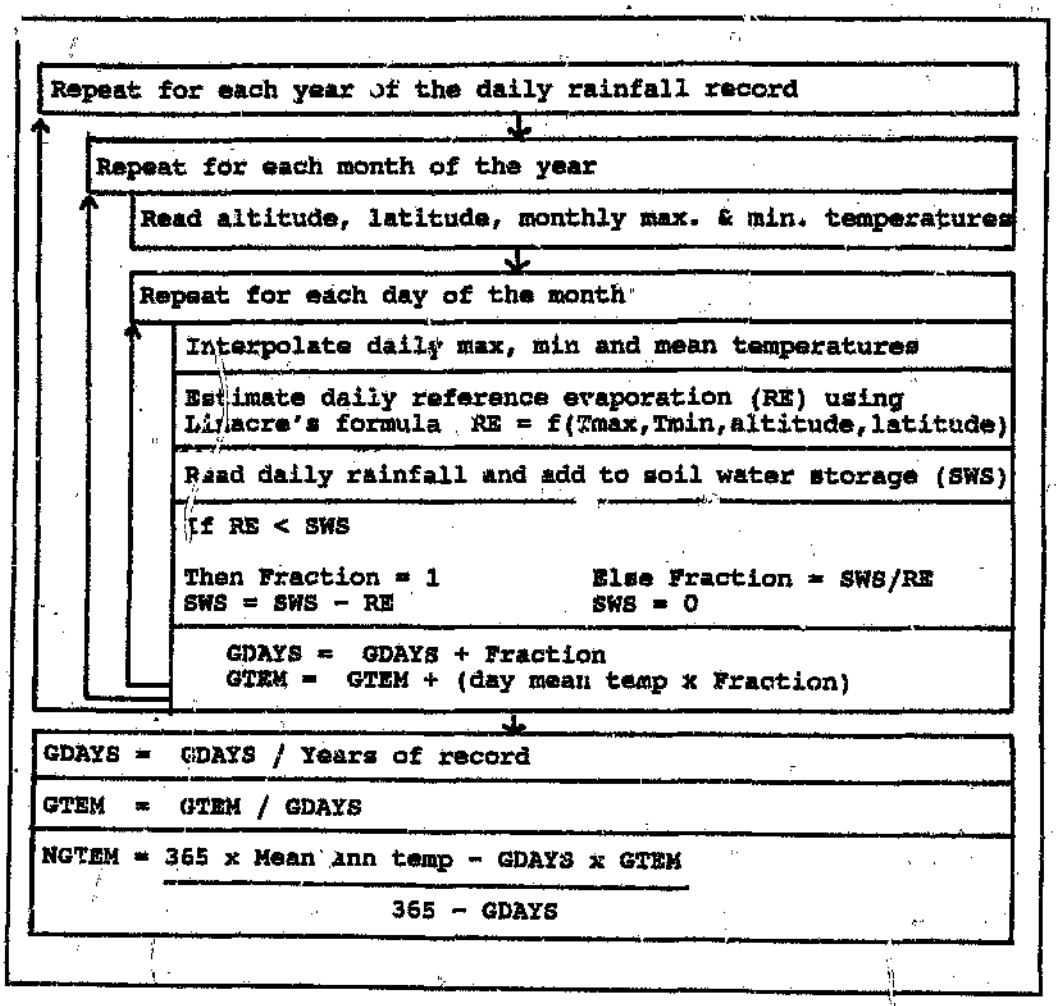


Figure 4.2: Schematic representation of the water balance model used to generate the indices of growth days (GDAYS), growth temperature (GTEM) and no-growth temperature (NGTEM).

'growth temperature' (GTEM; Fig. 4.2), giving an indication of energy supply when moisture is available for plant growth. It is equivalent to the mean wet season temperature. The mean temperature on days when moisture was not available for growth was recorded as 'no-growth temperature' (NGTEM). It can be considered as the mean dry season temperature. The terms 'growth temperature' and 'wet season temperature' are used interchangeably, as are 'no-growth temperature' and 'dry season temperature'. The difference between the wet and dry season temperatures (growth temperature minus no-growth temperature; TDIF) is an index of the season and degree of seasonality of rainfall. Positive values indicate summer rainfall and negative values indicate winter rainfall. The intensity of seasonality of rainfall in these seasons is indicated by the (absolute) value of this index.

The set of climatic indices, and the abbreviation used for each one are provided in Table 4.1. The list of weather stations and the biomes into which each was classified based on Rutherford & Westfall (1986), are presented in APPENDIX 1, together with the latitude and longitude of each station, mean annual precipitation, and values for the indices growth days, wet season temperature, dry season temperature and difference in temperature between the growth and no-growth seasons.

4.2.3 DATA ANALYSIS

As a basis for the selection of variables to be used in a model discriminating South Africa's biomes, all of the indices for each weather station were tabulated, and a stepwise discriminant analysis using forward selection (SAS 1985) was performed on the entire data set for each of the 163 weather stations. Selection was ended at the significance level of less than 0.10. The results were compared to the success achieved by Rutherford & Westfall's (1986) model.

4.3 RESULTS

4.3.1 USE OF DISCRIMINANT FUNCTION ANALYSIS AS A TOOL FOR THE SELECTION OF APPROPRIATE CLIMATIC VARIABLES

The order of selection of variables in the stepwise discriminant analysis (Table 4.2)

TABLE 4.1: The variables included in the stepwise discriminant function analysis, together with variable abbreviations used in tables that follow, as well as in the text.

Values obtained from records of the Weather Bureau

VARIABLE	ABBREVIATION
Mean annual rainfall	RAIN
Mean minimum temperature during the coldest month	JUT
Proportion of total rainfall during winter 6-month period	RWINT
Mean annual temperature	ANTEM
Summer aridity index	SAI
Summer half-year rainfall	SHYR

Values obtained from artificial rainfall data and water balance model

Duration of the growth season	GDAYS
Growth temperature	GTEM
No-growth temperature	NGTEM
Difference in temperature between growth and no-growth seasons	TDIF

TABLE 4.2: A summary of the stepwise discriminant function analysis showing the order of inclusion (STEP) of each climatic variable in the discrimination of the biomes of South Africa based on climatic indices, together with the partial correlation coefficients (PARTIAL R-SQUARED), F-statistics (F-STAT), and the significance of the F-statistics (PROB > F).

STEP	VARIABLE ENTERED	PARTIAL R-SQUARED	F-STAT	PROB > F
1	RWINT	0.899	279.2	0.0001
2	GDAYS	0.591	45.0	0.0001
3	SHYR	0.504	31.4	0.0001
4	GTEM	0.454	25.6	0.0001
5	RAIN	0.168	6.1	0.0001
6	TDIF	0.112	3.8	0.0029
7	ANTEM	0.088	2.9	0.0166
8	JUT	0.109	3.6	0.0041
9	SAI	0.067	2.1	0.0698

illustrates the relative contribution of each to the discrimination of South Africa's biomes. The first variable to be included was the proportion of rainfall occurring in winter (RWINT), this being the same index used in Rutherford & Westfall's (1986) study, separating the summer and winter rainfall areas. This index was highly correlated to other indices (Table 4.3), including the difference in temperature between the growth and no-growth seasons (TDIF). Both of these indices provide a measure of the season in which rain falls, and separates biomes in the summer and winter rainfall areas. To a lesser extent it was correlated to the summer aridity index (SAI) used by Rutherford & Westfall (1986), with winter rainfall areas and the nama-karoo biome having low values for this index. The summer aridity index is useful in discriminating wet and dry areas within the summer rainfall biomes, but it does not discriminate biomes in winter rainfall areas from other arid biomes. The most statistically significant index in the analysis reflects the season in which rain falls.

The second variable to be included was the duration of the growth season (GDAYS, Table 4.2), an index derived from the water balance model indicating the duraton of the growth season based on moisture availability. This index separates the arid and mesic biomes. Once again it was highly correlated to another index (Table 4.3), mean annual rainfall (RAIN). The advantage of using the index GDAYS rather than any measure of rainfall (such as during the summer or winter half year periods, or any other portion of the year - such as in the summer aridity index) is that it integrates the supply (rainfall) and demand (potential evaporation) components of the water balance. The relationship between this index (GDAYS) and mean annual rainfall (RAIN) for example, indicates that for a given rainfall, there is great variation in the duration of the growth season (Fig. 4.3), and that it is mainly dependant on the season in which rain falls.

The third variable to be included in the discriminant function analysis was the rainfall during the summer half-year period (SHYR, Table 4.2), the same index used by Rutherford & Westfall (1986). The value of this index in the present analysis is in separating biomes along a moisture gradient in the summer rainfall areas. It is redundant to some extent, with the separation of summer and winter rainfall areas having been achieved by selection of the first variable, the proportion of rain falling in winter (RWINT), and the separation of biomes along a moisture gradient within

TABLE 4.3: Pearson's correlation coefficients for the climatic variables used in the stepwise discriminant analysis of South Africa's biomes. Correlation coefficients that are significant ($P < 0.01$) are underlined.

	RAIN	ANTEM	GDAYS	GTEM	JUT	NGTEM
ANTEM	-0.12					
GDAYS	0.81	-0.17				
GTEM	0.03	0.73	-0.30			
JUT	0.16	0.78	0.30	0.38		
NGTEM	-0.18	0.92	-0.05	0.47	0.77	
SAI	-0.62	0.01	-0.19	-0.51	0.07	0.26
SHYR	0.80	-0.02	0.37	0.37	0.05	-0.29
TDIF	0.18	0.00	-0.28	0.66	-0.25	-0.34
RWINT	-0.20	-0.10	0.29	-0.71	0.18	0.23

	SAI	SHYR	TDIF
SHYR	-0.86		
TDIF	-0.76	0.64	
RWINT	0.82	-0.68	-0.96

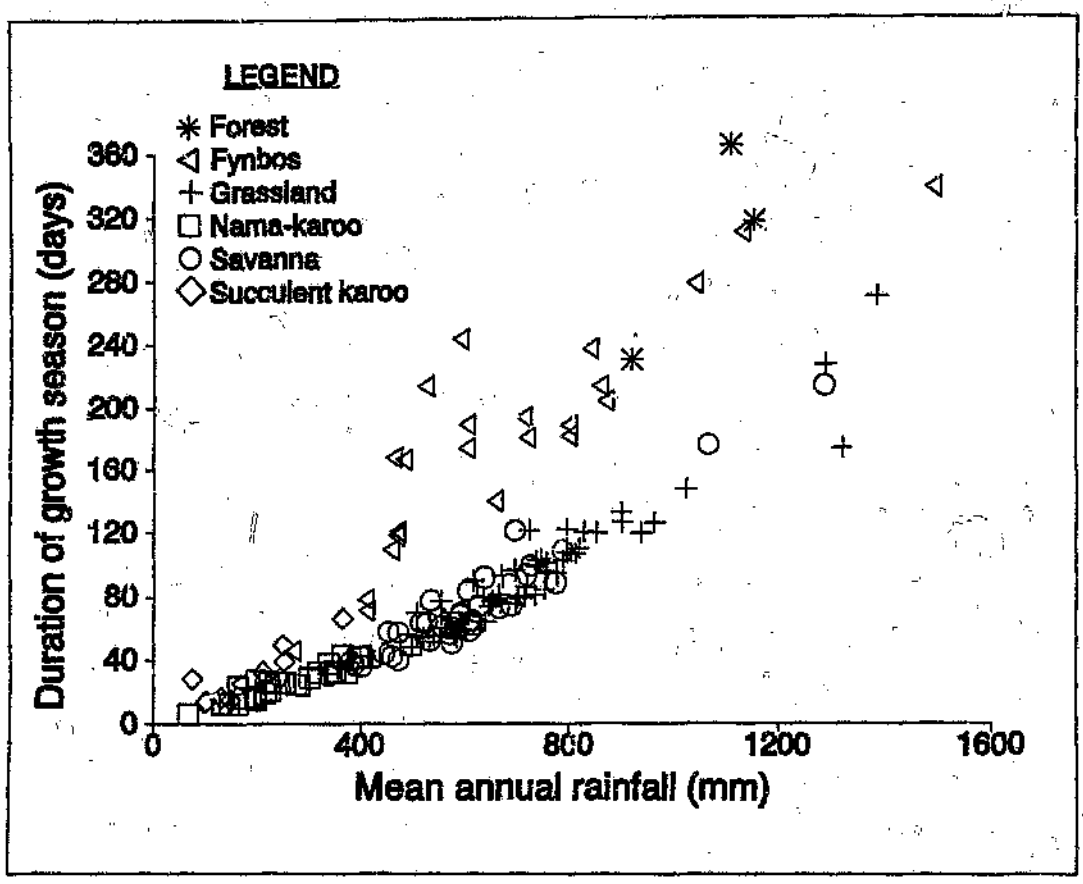


Figure 4.3: The distribution of weather stations in known biome types in relation to mean annual rainfall and mean number of days of growth opportunity.

each of the summer and winter rainfall areas by selection of the second variable GDAYS. It is also correlated to mean annual rainfall (RAIN) and the summer aridity index (SAI; Table 4.3).

The next variable to be included was the temperature during the growth season (GTEM, Table 4.2), this being an index derived from the water balance model and indicating energy supply during the season in which moisture is available for plant growth. It is conceptually related to Rutherford & Westfall's (1986) summer aridity index (SAI), which is a measure of moisture availability during the warmest four months of the year, or the months of the year when energy supply is greatest. The advantage of using the index GTEM, derived from the water balance model, is that it is not fixed to a somewhat arbitrarily defined four month period, but estimates energy supply when moisture is in fact available for plant growth.

The remaining variables contribute relatively little to the discrimination of South Africa's biomes, as illustrated by comparison of the partial R^2 values and success rates associated with inclusion of successive variables in the discriminant analysis (Table 4.2).

The problems of using an approach such as a discriminant function analysis in selecting variables for inclusion in a model discriminating South African biomes are that it lacks an intuitive conceptual base, that it is designed to minimise the number of variables, and that it does not consider each variable independantly of or jointly with others (SAS 1985). It has nevertheless been useful in extracting the features of climate that contribute most to separation of South Africa's biomes. These are the season in which rain occurs, the duration of the growth season based on water supply, and the temperature during the growth season.

4.3.2 SELECTION OF VARIABLES

On the basis of the order of inclusion of climatic indices in the discriminant function analysis, the most important features of climate associated with the discrimination of South Africa's biomes have been recognised. Instead of using a single variable to achieve the discrimination betwen summer and winter rainfall areas, as in the

discriminant function analysis, the plot of temperature during the growth and no-growth seasons (Fig. 4.4) gives an indication of both the season in which rain falls and the strength of the seasonality of rainfall. These indices are largely independant of one another (Table 4.3), and therefore suitable for a 'most parsimonious' set. Points on the plane in which the growth temperature is greater than the no-growth temperature experience summer rainfall, while those in which the no-growth temperature is greater than the growth temperature experience winter rainfall. Where the two are approximately equal the rainfall is aseasonal. The grassland, nama-karoo and savanna biomes receive rainfall in summer, while the fynbos and succulent-karoo biomes receive rainfall in winter. The forest biome receives rainfall throughout the year.

The duration of the growth season is a useful discriminant between the arid biomes (nama-karoo and succulent karoo), the semi-arid biomes (fynbos, grassland and savanna) and the humid biome (forest). Within the summer rainfall area, nama-karoo has a shorter growth season than the grassland and savanna biomes (Fig. 4.5). It is evident however, that the duration of the growth season and the temperature during the dry season interact in defining the boundary between nama-karoo and grassland and savanna; grasslands and savannas appear to require a longer growing season as the dry season temperature decreases. This illustrates the stressful effect of low temperatures in the dry season in limiting the distribution of elements from the more mesic biomes in summer rainfall areas, providing an indication of the metabolic cost of cold temperatures in the dry season.

Similarly there appears to be an interaction of the dry season temperature and duration of the growth season in the winter rainfall areas in separating the fynbos (mesic) and succulent-karoo (arid) biomes (Fig. 4.6). In contrast to the summer rainfall areas however, as the dry season temperature increases an increase in the duration of the growth season is required to support fynbos. This illustrates the stressful effect of high dry season temperatures in limiting the distribution of the more mesic elements in winter rainfall areas, indicating the metabolic cost of high temperatures that cannot be regulated by transpiration and therefore be met by photosynthesis.

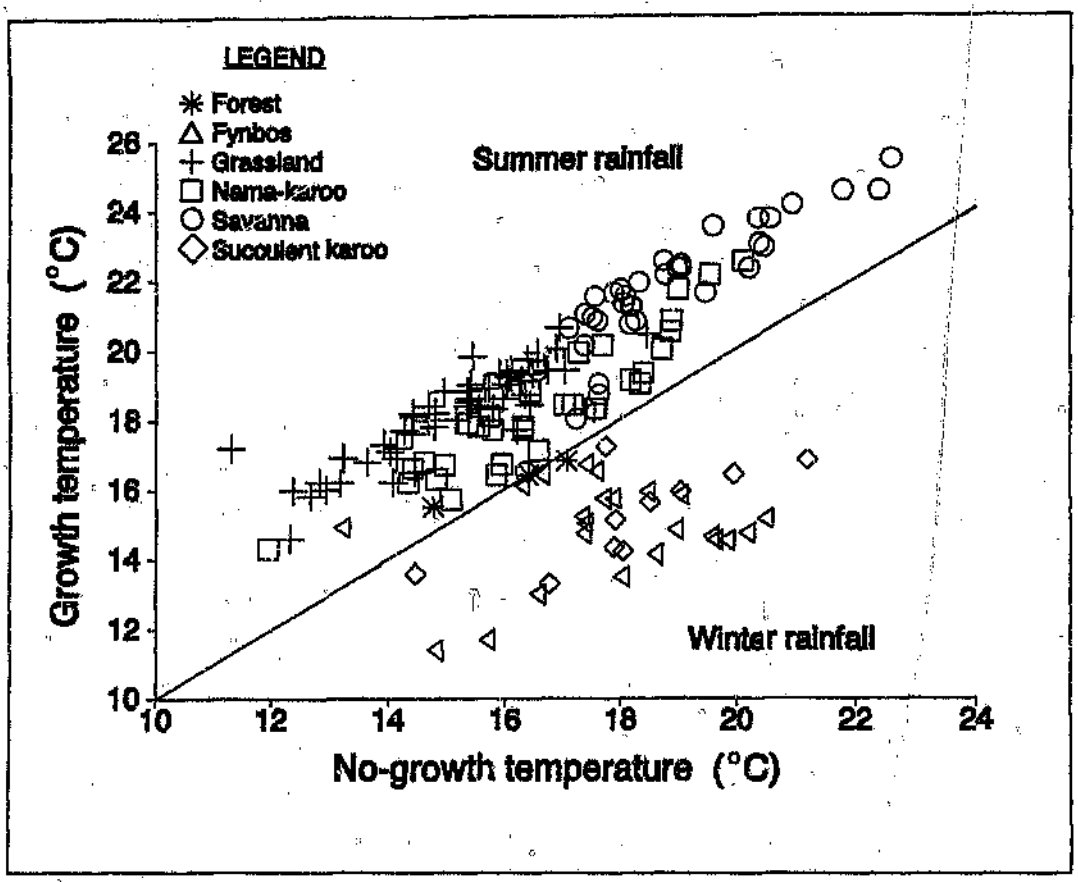


Figure 4.4: The distribution of weather stations in known biome types in relation to the temperature during the growth and no-growth seasons.

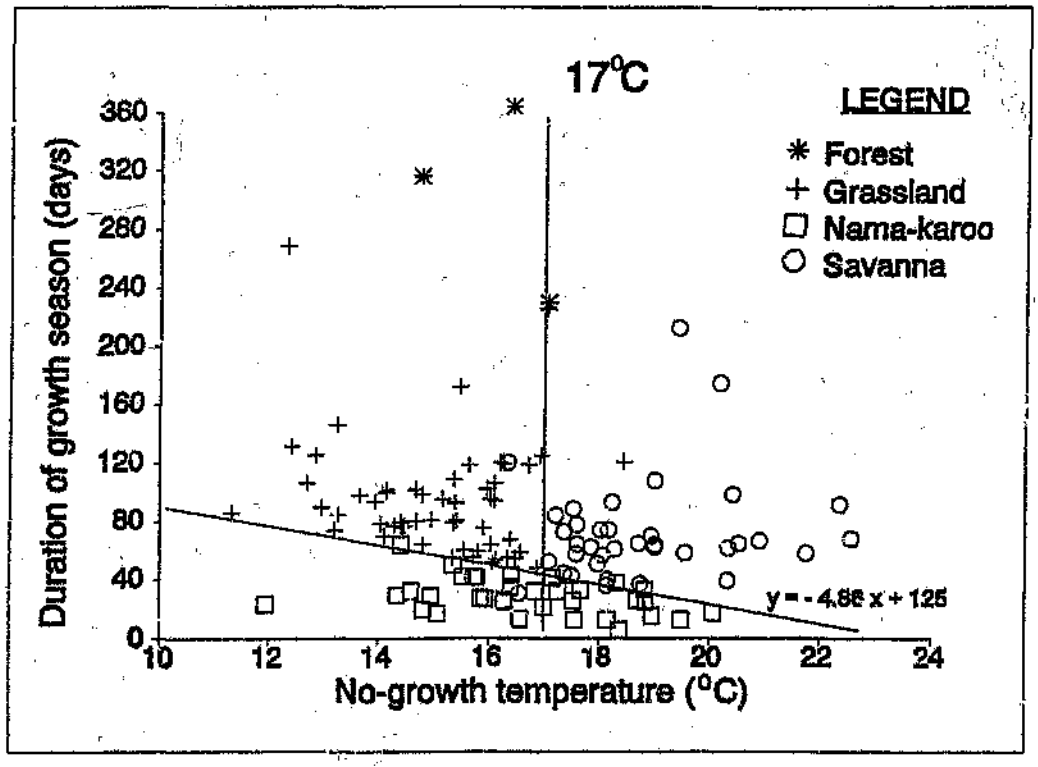


Figure 4.5: The distribution of weather stations in the summer rainfall biomes (grassland, nama-karoo and savanna) and in the biome in which rainfall is aseasonal (forest) in relation to the temperature during the no-growth season and the duration of the growth season.

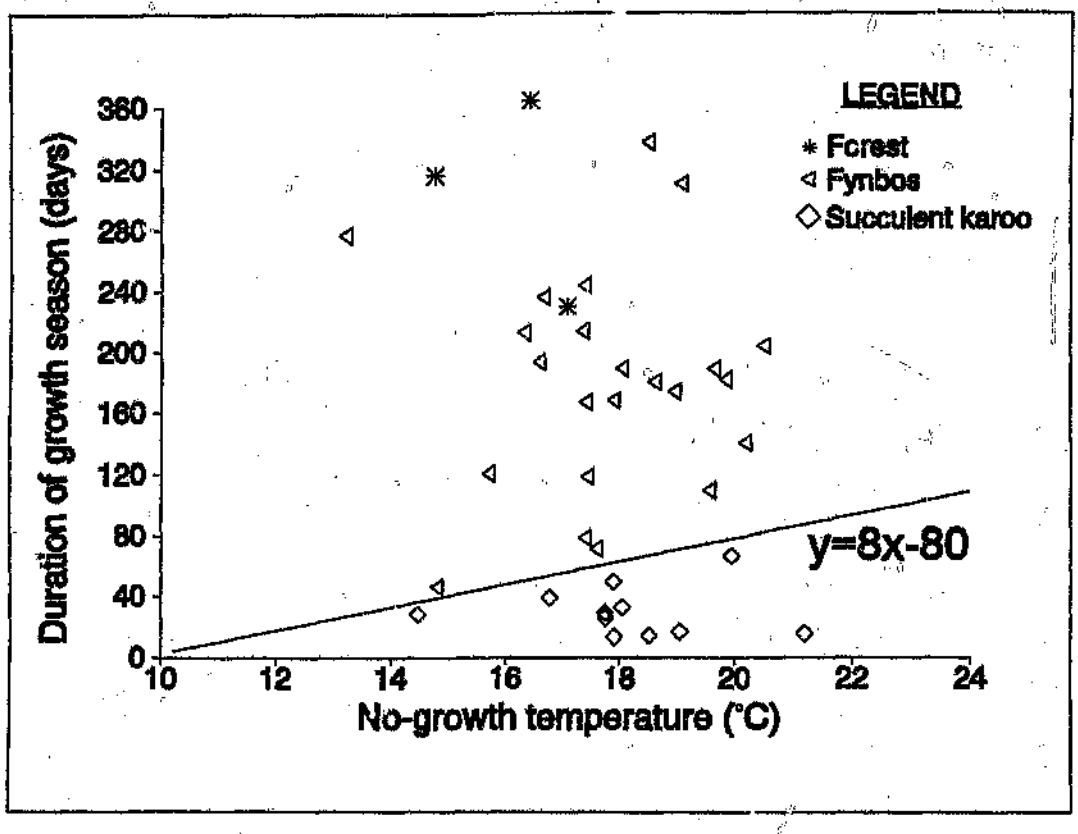


Figure 4.6: The distribution of weather stations in the winter rainfall biomes (fynbos and succulent karoo) and in the biome in which rainfall is aseasonal (forest) in relation to the temperature during the no-growth season and the duration of the growth season.

The grassland biome may be differentiated from the savanna biome by the mean temperature during the dry season (Fig. 4.5). Stations in the grassland biome have a mean dry season temperature less than or equal to 17.0°C, while savannas have a mean dry season temperature greater than this. Only three stations out of the 93 in these two biomes were exceptions to this rule. The mean temperature during the growth season is also generally lower in the grassland than in the savanna biome, but discrimination is weaker.

The forest biome in South Africa has a patchy and restricted distribution, and the number of weather stations that can be used to evaluate the climatic correlates of its distribution is small. Three stations from large forest patches within the broad extent grassland and savanna biomes have therefore been used in the present analysis, as well as three stations from extensive forest areas. A measure of the degree of seasonality of rainfall is provided by the difference between growth and no-growth temperatures (Fig. 4.7a). There is clearly a lower limit in terms of the duration of the growing season to which forest will extend (about 210 growth days per annum), and on the basis of the limited sample, there would appear to be an increase in the duration of the growth season required to support forest as the degree of seasonality of the growth season increases. The plane depicted in Figure 4.7a is just a graphical reorientation of a three dimensional plot of the indices used thus far (NGTEM, GTEM and GDAYS), with the duration of the growth season (GDAYS) added as a third dimension to the plane of growth and no-growth temperature as shown in Figure 4.4. The relationship between the distribution of forest patches and these three indices is indicated in Figure 4.7b, in which isolines of the duration of the growth season required to support forest patches under a given growth- and no-growth temperature combination are illustrated.

The discrimination of South Africa's biomes can be achieved based on three indices: the temperatures during the growth and no-growth seasons, and the duration of the growth season. A model of biome distribution based on these three indices, and using the relationships described above and illustrated in Figures 4.4 - 4.7, is presented in the form of a decision tree (Fig. 4.8). The success of the decision tree in predicting the biome types used in the present analysis is presented in Table 4.4. Only ten sites out of 163 were misclassified.

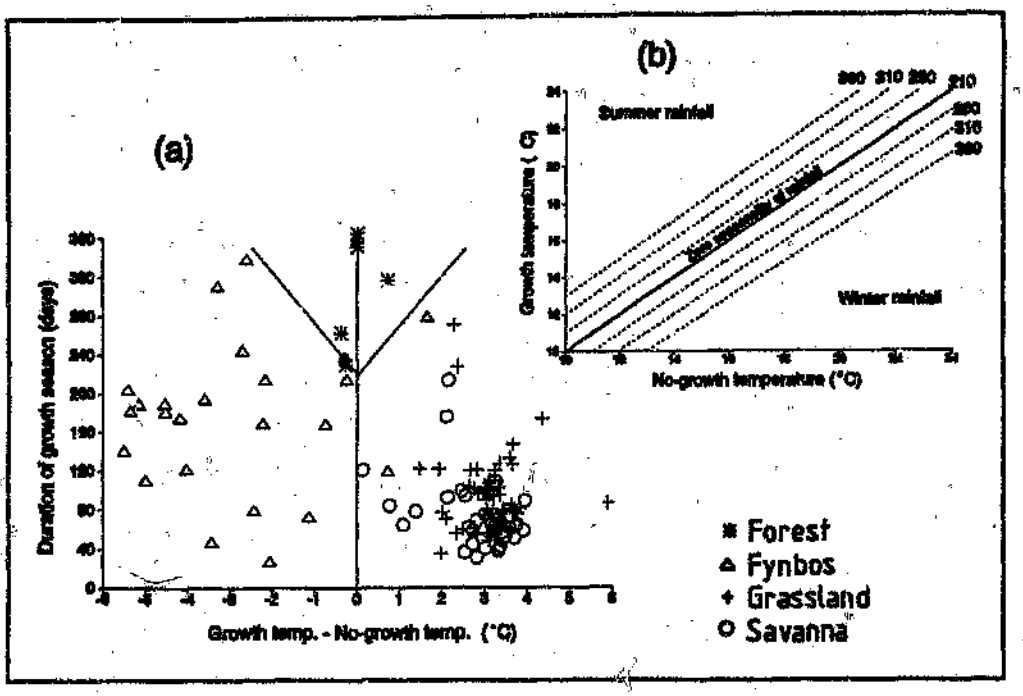


Figure 4.7: The distribution of weather stations in relation to the difference in temperature between the growth season and the no-growth season and the duration of the growth season (a). The temperature index provides an index of both the seasonality (positive in summer rainfall biomes, negative in winter rainfall biomes) and the degree of seasonality of rainfall (aseasonal where the temperature index is zero, with the degree of seasonality increasing as the absolute value of this index increases). Forest requires an increase in moisture availability as the degree of seasonality of rainfall increases, a relationship illustrated for the indices of growth temperature and no-growth temperature by means of isolines in the inset (b).

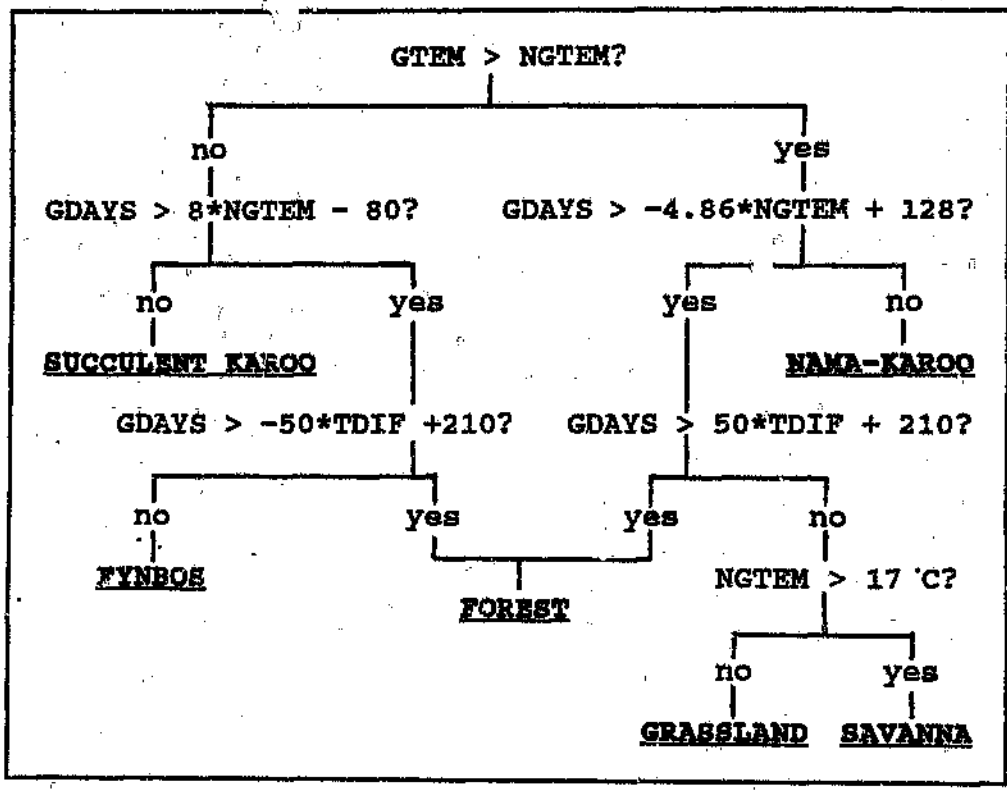


Figure 4.8: A decision tree used to discriminate South Africa's biomes on the basis of climatic indices.

TABLE 4.4: The success of the model discriminating the biomes of South Africa based on the decision tree presented in Figure 4.8 for sites that were classified into one of six biomes according to Rutherford & Westfall (1986). Sites correctly predicted are indicated in bold.

Biome classification according to the map of Rutherford & Westfall (1986)	Classification into biome type based on the decision tree (Fig. 4.8)					
	Forest	Fynbos	Grass-land	Nama-karoo	Savanna	Succul. karoo
Forest (n=3)	**3**	0	0	0	0	0
Fynbos (n=23)	1	**20**	1	0	1	0
Grassland (n=55)	0	0	**53**	0	2	0
Nama-karoo (n=34)	0	0	1	**32**	1	0
Savanna (n=37)	0	0	1	2	**34**	0
Succulent karoo (n=11)	0	1	0	0	0	**10**

4.3.3 COMPARISON OF THE TWO SOUTH AFRICAN APPROACHES

The success of the present exercise is independantly evaluated by comparison with the success of Rutherford & Westfall's (1986) approach (Table 4.5). The present discrimination of biome types compares well with the attempt of Rutherford & Westfall (1986), who based their categorization of South Africa's biomes on four indices.

4.4 DISCUSSION

4.4.1 THE BIOLOGICAL INTERPRETATION OF INDICES USED IN THIS STUDY

The indices developed in this study correlate well with the distribution of South Africa's biomes. They also appear well founded biologically. The concept 'days of growth opportunity', integrates both the supply-side (precipitation) and the demand-side (potential evaporation) of plant water relations. It is therefore expected to be more robust than indices derived from rainfall or evaporation data alone (cf. Holdridge 1967, Whittaker 1975, Mather & Yoshioka 1968, Rutherford & Westfall 1986). In addition to having an influence on the water balance, temperature has direct biological effects. The index of temperature during the wet season gives an indication of its effect as a regulator of physiological processes, and is conceptually related to using a temperature growth response curve as an index of favourability during the wet season (cf. Specht 1981), or to the concept of biotemperature (Holdridge 1967). On days when water is not available for plant growth, temperature provides an indication of metabolic costs that cannot be met by active photosynthesis, or of heat stress that cannot be regulated by transpirational cooling. One or other of these stresses is more important depending on the temperature conditions prevalant during the dry season. In the winter rainfall areas where the dry season temperatures are high, the effect of heat stress that cannot be regulated by transpiration is the more important of the two constraints. In the summer rainfall areas however, the major metabolic stress of cold temperatures during the dry season would be that it limits active photosynthesis. It may also be an indirect measure of the frequency of frost.

TABLE 4.5: A comparison of error rates (number misclassified as a proportion of the total number of sites) for the weather stations used to discriminate South Africa's biomes in this study, using variables selected in this study, and in the study of Rutherford & Westfall (1986). Three variables were used in the present study compared with the four in the study of Rutherford & Westfall (1986).

STUDY	VARIABLES INCLUDED	ERROR RATE
Present	GTEMP NGTEMP GDAYS	0.061
Rutherford & Westfall (1986)	JUT SAI SHYR WINT	0.151

4.4.2 THE IMPORTANT FEATURES OF A GRASSLAND CLIMATE

The essential features of climate that determine the distribution of South Africa's grasslands are the presence of:

- a moderate water supply, but not sufficient to eliminate seasonality;
- warm temperatures during the wet season; and
- a cold dry season.

Aspects of this climate have been linked to the distribution of grasslands elsewhere in the world (Weaver & Clements 1938. Borchert 1950, Thornthwaite 1952, Stephenson 1990).

A feature overlooked in past studies that have addressed the same problem has been that they have generally focussed on boundaries with one or other of the adjacent biomes, and drawn more generalised conclusions than warranted. The boundary with savanna is related to the temperature during the dry season. Grasslands have a cooler dry-season temperature than savannas. The cold temperatures in the grassland biome cited by Acocks (1975) as limiting the establishment of woody plants, may indeed explain the absence of savanna trees from the grassland biome. However, the cold dry season temperature associated with the grassland biome does not explain the absence of nama-karoo woody plants from the grassland biome, as these are able to withstand the entire range of dry-season temperatures encountered within the grassland biome (Fig. 4.5). Is it that nama-karoo plants are unable to tolerate moist conditions, or are they unable to compete with grassland plants under moist conditions?

4.4.3 THE ROLE OF ANTHROPOGENIC FACTORS

The suggestion by Acocks (1975) that there has been invasion at a biome-wide scale of grassland by nama-karoo in the region presently occupied by 'false upper karoo' (veld type 36; Fig. 4.9) as a result of pastoral activity, is examined in the light of the present study. If there has been a change in physiognomy as a result of pastoral activities in the past, then it might be expected that there will be little correlation between climate and the distribution of these two biomes. This issue has been examined in greater detail by distinguishing all weather stations from the false upper

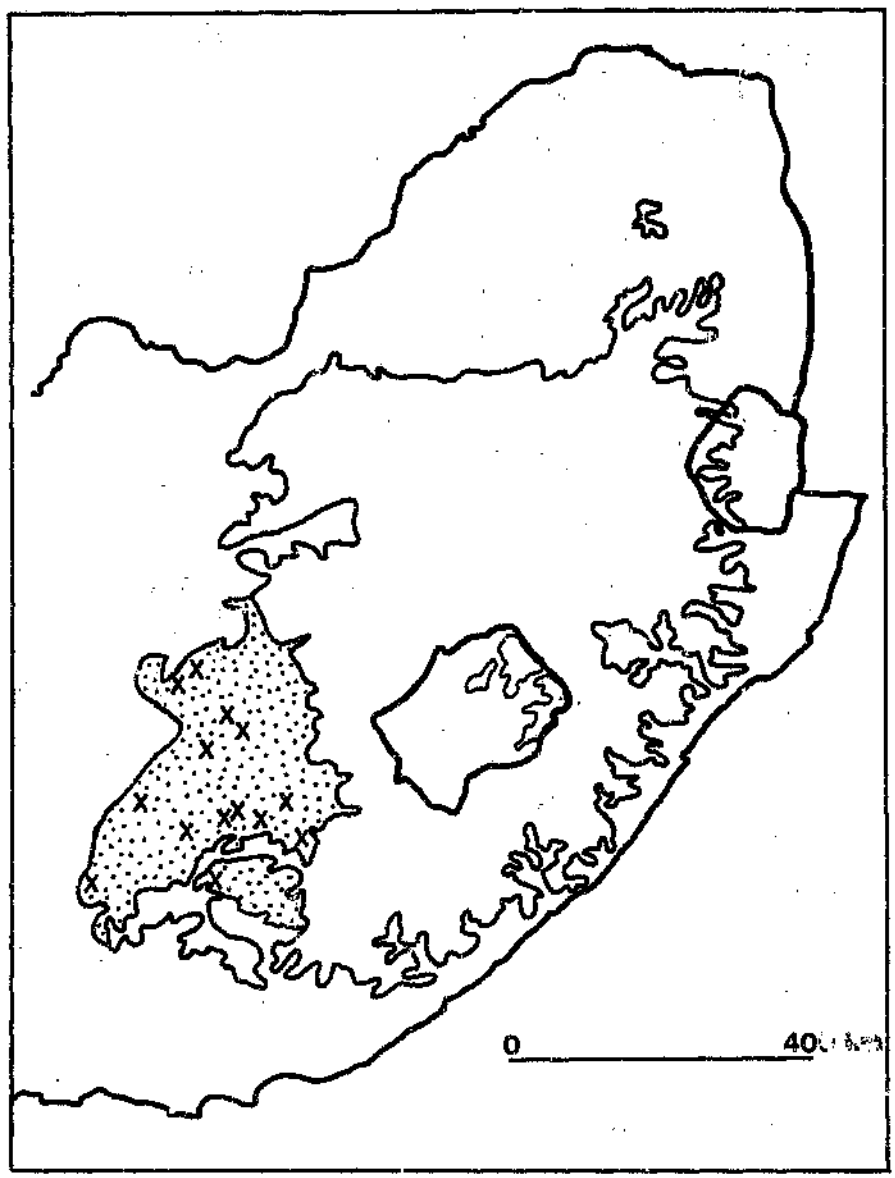


Figure 4.9: The approximate distribution of Acock's (1975) False Upper Karoo (stipples) in relation to the grassland biome, showing the location of weather stations (X) used to discriminate what Acocks considered to be the grassland biome prior to settlement of the subcontinent by agropastoralists.

karoo from those in the grassland, nama-karoo and savanna biomes, and examining their distribution in relation to other summer rainfall biomes. The results of this exercise are illustrated in Figure 4.10. If Acocks's (1975) suggestion that the grassland biome has been invaded by karoo in the region presently occupied by the false upper karoo is correct, then the present biome classification based on climatic indices (Fig. 4.8) is incorrect not only with respect to the boundary between the grassland and nama-karoo biomes, but also with respect to the boundary between these two biomes and the savanna biome (Fig. 4.11).

Although as successful as the discrimination of biomes if invasion is not assumed (Table 4.6), their discrimination is not biologically intuitive. The increase in the duration of the growth season required to support the more mesic of the summer rainfall biomes as the dry season temperature decreases is biologically intuitive (cf. Fig. 4.5 and Section 4.4.1). The climatic boundary between the nama-karoo and grassland biomes (assuming the false upper karoo to be part of the grassland biome) shows no evidence of this relationship, and is therefore biologically counter intuitive. It is therefore argued that it is not necessary to assume that the false upper karoo is anything more than a slightly mesic nama-karoo. It is further suggested that before broad-scale vegetation distribution can be attributed to human or other disturbance, the possibility that their distribution can be accounted for purely on climatic grounds must be conclusively dismissed. This is supported by the study of Hoffman & Cowling (1990), who suggest that the boundary between nama-karoo and grassland oscillates in response to climatic fluctuations.

4.5 SUMMARY

The distribution of South Africa's grassland biome has been predicted on the basis of three climatic indices derived from a water balance model. The indices were the duration of the growth season (GDAYS), the mean temperature during the season when sufficient soil water was available for plant growth (GTEM) and the temperature during the season when the soil was dry (NGTEM). Based on these indices it was possible to separate the summer and winter rainfall biomes, with fynbos and succulent karoo in winter rainfall areas, and grassland, nama-karoo and savanna in summer rainfall areas. The succulent karoo and nama-karoo biomes were the more

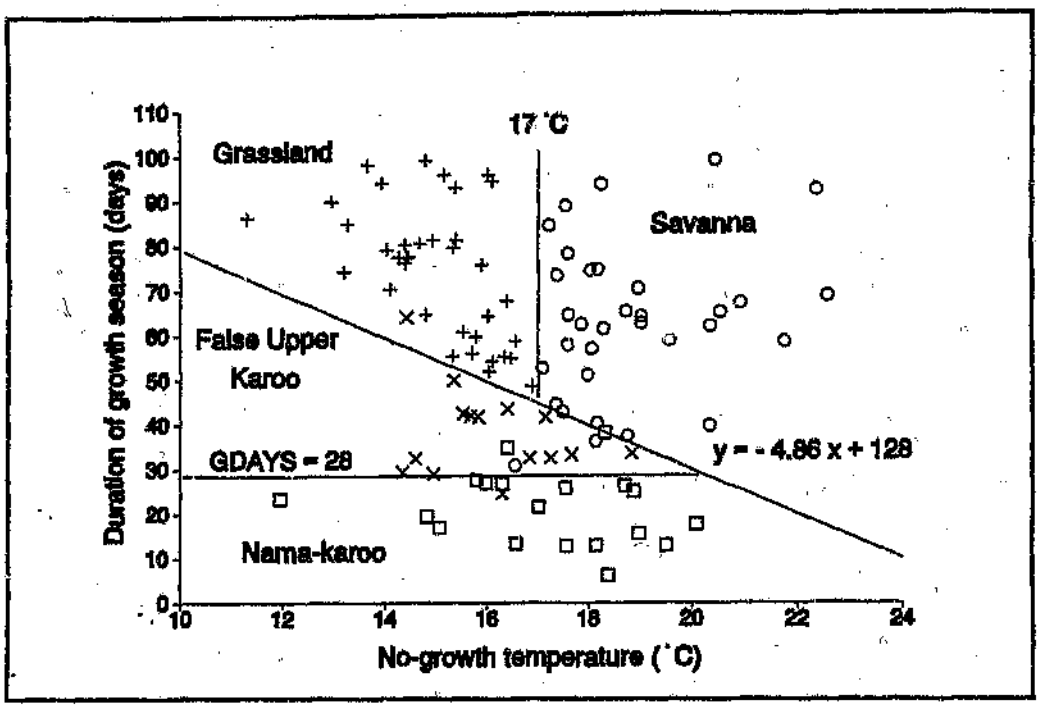


Figure 4.10: The distribution of weather stations in the grassland (+) and savanna (o) biomes close to their climatic boundary with the nama-karoo. Stations in the nama-karoo biome (□) as mapped by Rutherford & Westfall (1986) were distinguished from those in the Acock's (1975) False Upper Karoo (x), as indicated in Figure 4.9, in an attempt to investigate the role of climate in determining the distribution of the grassland biome as envisaged by Acocks (1975) prior to settlement of the subcontinent by agropastoralists.

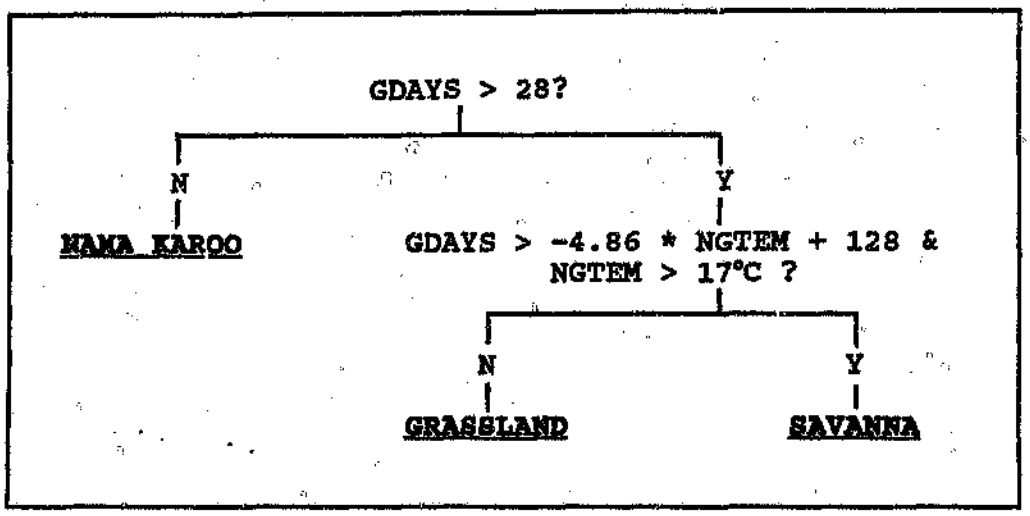


Figure 4.11: Decision tree depicting the discrimination of nama-karoo from savanna and grassland assuming that grassland has been converted to nama-karoo in the region of Acocks's (1953) False Upper Karoo as a result of human activity.

TABLE 4.6: The success of the model discriminating the grassland, nama-karoo and savanna biomes based on the decision tree presented in Figure 4.11, assuming that the grassland biome has been invaded by nama-karoo in the region of the False Upper Karoo as described by Acocks (1975).

Biome classification following Acocks (1975)	Classification into biome type based on the decision tree (Fig. 4.11)		
	Grassland	Nama-karoo	Savanna
Grassland (n=69)	66	1	2
Nama-karoo (n=20)	1	18	1
Savanna (n=37)	2	0	35

arid biomes in these two rainfall areas respectively. The savanna biome occurs in areas that have a warmer dry season than the grassland biome. The forest biome occurs in areas with a small water deficit in which rainfall is only weakly seasonal. The presence of moderate quantities of rainfall in summer when temperatures are favourable for plant growth, together with seasonal drought in the cold season are important features of the climate of the grassland biome.

The suggestion that the grassland biome has been invaded by nama-karoo vegetation was examined indirectly by investigating the climatic boundaries between these two biomes assuming the distribution of grasslands proposed by Acocks (1975). The boundary is relatively clear, but is not biologically intuitive, and it therefore appears that invasion has not taken place to the extent suggested by Acocks (1975). Based on this evidence it is suggested that before anthropogenic modification of vegetation at a biome-wide scale is invoked, it should be demonstrated that it cannot be accounted for based on climatic grounds.

CHAPTER 5

THE DISTRIBUTION OF WOODED PATCHES WITHIN THE GRASSLAND BIOME

5.1 INTRODUCTION

The biomes of South Africa have been rigorously defined on the basis of physiognomic criteria (Rutherford & Westfall 1986), and they are mapped as homogeneous units with abrupt boundaries. In reality the flora of a given biome contains inclusions from neighbouring biomes. Within the area mapped as the grassland biome there are patches of forest, fynbos, nama-karoo and savanna. The inclusion of these is due to the superimposition of smaller-scale influences on the congruence of predominant life-forms and climate recognised at the subcontinental scale, including microclimate, edaphic conditions and disturbance regimes. The objective of this part of the study was to identify conditions under which woody plants become locally dominant within the grassland biome.

Rutherford & Westfall's (1986) discrimination of biomes was based on physiognomy alone. These differences are associated with floristic differences, generally above the species level (Gibbs Russell 1987). When considering patches of woody elements within the grassland biome, mixtures of elements from two neighbouring biomes frequently occur. Based on the use of physiognomic criteria alone such sites may be classified into a vegetation unit unrelated to either of the two whose members are represented. For example, the presence of phanerophytes, chamaephytes and hemicryptophytes is the combination of life-forms that distinguishes the fynbos biome (Rutherford & Westfall 1896), but this combination of life-forms occurs in situations where there is a mixture of savanna and nama-karoo elements, such as at the nama-karoo - savanna boundary. Rutherford & Westfall (1986) recognised this problem, and termed the vegetation at the nama-karoo - savanna boundary 'pseudofynbos'. This vegetation type is neither floristically related to true fynbos, nor could it possibly be determined by the same climatic features, with rainfall in the fynbos biome in winter, but in both the nama-karoo and savanna biomes it is in summer. This illustrates the weakness of using physiognomic criteria alone to discriminate

vegetation types at a more detailed scale of resolution than the biome-wide scale. In recognition of this problem, the basis for discriminating the affinity of wooded patches in the grassland biome in this study has been approached using floristic criteria rather than structural differences.

5.2 METHODS

5.2.1 COLLECTION OF DATA IN THE FIELD

A total of 70 sites were visited in nine study areas within the grassland biome (Fig. 5.1a). The study areas were selected to cover a wide range of temperature and moisture conditions (Fig. 5.1b). Within each study area, sites were chosen to cover a wide range of plant communities. The number of plants per hectare for each species of woody plant was estimated for each species using the point-to-plant and plant-to-nearest-neighbour method of Cox (1976). Aerial cover of woody elements was estimated by measuring the longest and shortest cross-sectional diameters of each woody plant encountered, and estimating aerial cover assuming that the projected canopy was an ellipse. Site characteristics measured were: slope (clinometer); aspect to the nearest 45° (compass); and microrelief (by measuring the height at 2 m intervals along a string pulled taut between two stakes 20 m apart, each the same height above the ground). Fire frequency and grazing intensity were each scored on a scale from 1 to 5 based on information obtained from the landowner about stocking rates, the system of paddocking, and burning frequency. A soil profile description was carried out in a soil pit either to bedrock or to a depth of 1.3 m (whichever was the shallower). Soil samples were taken at depth intervals within each horizon depending on the thickness of each horizon, and composite samples of 25 randomly located subsamples were taken from the A-horizon to a depth of 10 cm.

5.2.2 SOIL ANALYSES

Soil texture was measured for each soil sample using the hydrometer method (Anderson & Ingram 1989). Bulk density was measured by coating intact peds of known mass with wax, and measuring their volume (Anderson & Ingram 1989). Organic carbon was determined using the technique of Nelson & Sommers (1975).

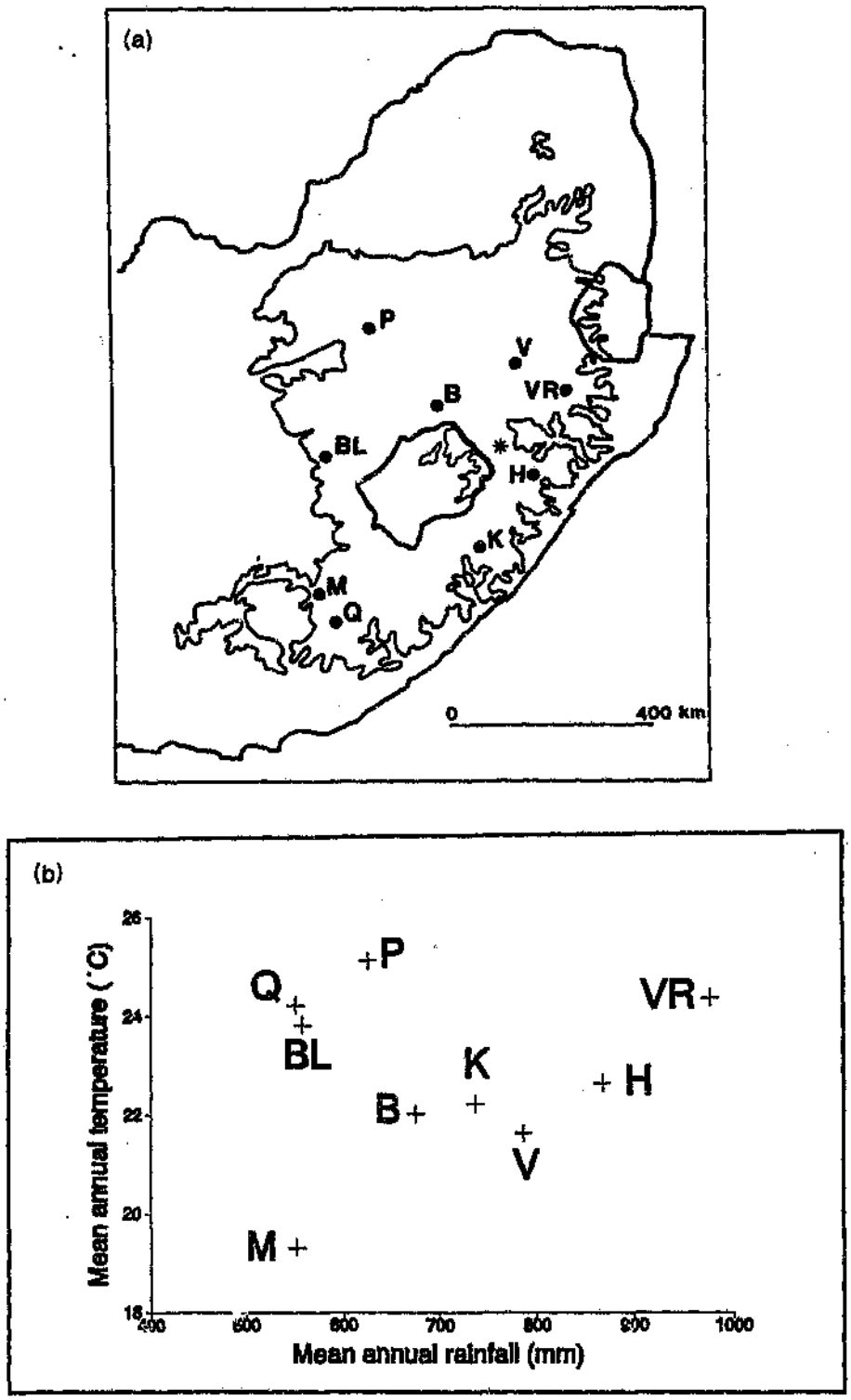


Figure 5.1: The distribution of study areas within the grassland biome (a) and the range of mean annual temperature and precipitation covered by the selection of these sites (b). Abbreviations for the place names and the number of stations at each site are as follows: B = Bethlehem, 8; BL = Bloemfontein, 9; H = Howick, 6; K = Kokstad, 7; M = Marshmoor, 6; P = Parys, 10; Q = Queenstown, 9; V = Volksrust, 8; VR = Vryheid, 7. The location of Thabamhlope is shown as an asterisk.

5.2.3 CLIMATIC MODELLING

The effects of altitude, slope and aspect on the water balance were accounted for as far as possible (Fig. 5.2). This was done by estimating temperature conditions at the site from records from the nearest weather station, modified by altitude, slope and aspect using the program MTCLIM (Running et al. 1987). MTCLIM modifies mean daily maximum and minimum temperatures taken from nearby weather stations (less than 5 km away) for altitude using a lapse rate, and for latitude, slope and aspect by calculating the difference in net shortwave radiation between the site (known latitude, altitude, slope and aspect) and that of a flat surface of the same latitude and altitude, using the empirical relationship described by Garnier & Ohmura (1968).

The effects of soil water holding properties on the water balance were also included (Fig. 5.2). The program RETFIT (J. Hutson, Personal Communication[1]) calculates the soil water content at different water potentials based on empirical relationships determined for these variables based on texture (percentage sand, silt and clay), organic carbon content, and bulk density. Water contents at field capacity (-0.3 MPa) and wilting point (-15 MPa) were calculated. The modified daily maximum and minimum temperatures and the soil water contents at field capacity and wilting point were included in a modification of the water balance routine described in the previous chapter, as illustrated in Figure 5.3. The moisture inputs as rainfall were determined using daily rainfall data for a local station (less than 5 km from each site) using the program GENRAIN (Zucchini & Adamson 1984). This was added to the soil profile from above until the profile had been filled to field capacity. Excess water was considered lost as runoff or deep drainage. Plants were considered to extract the amount of water in the soil profile until wilting point was reached. Water demand was calculated using Linacre's (1977) procedure for estimating monthly potential evaporation. As in the previous chapter, the duration of the growth season (GDAYS), the growth season temperature (GTEM) and the no-growth season temperature (NGTEM) were calculated.

Variables for each site included in data analysis are summarised in Table 5.1.

---

[1] J. HUTSON, Cornell University, Ithaca, New York, USA.

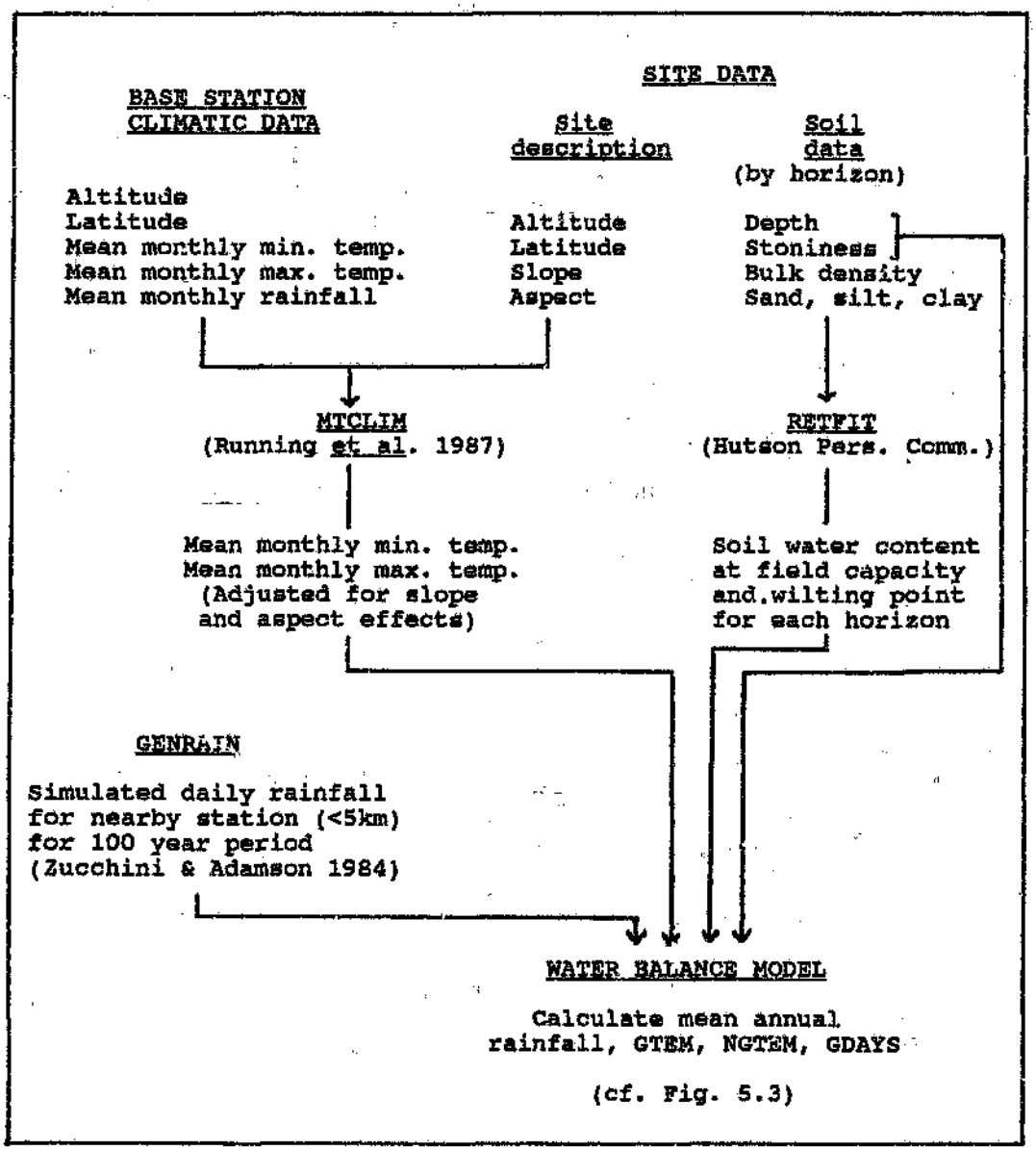


Figure 5.2: Outline of techniques used to determine local site climatic conditions (see text for details).

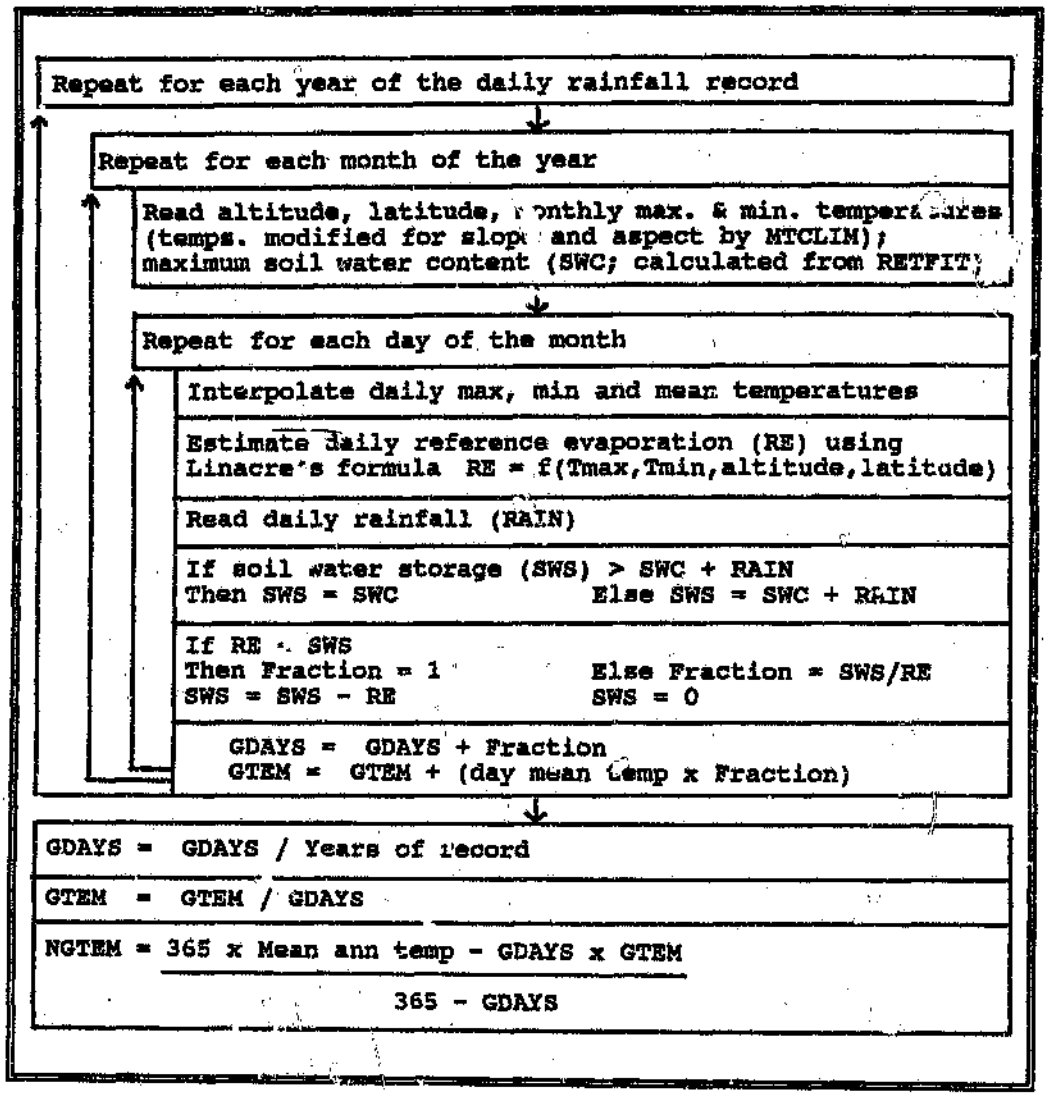


Figure 5.3: Schematic representation of the water balance model used to generate the indices of growth days (GDAYS), growth temperature (GTEM) and no-growth temperature (NGTEM), and including the effects of soil moisture properties.

TABLE 5.1: Environmental variables determined for each study site together with abbreviations used in the text and in tables and figures that follow.

Site characteristics measured in the field		
Slope	SLOPE	(degrees)
Aspect		
Slope evenness	SDSLO	(sd units)
Fire frequency	FIRE	(years)
Grazing intensity	GRAZ	(5 classes)
Depth of soil profile	SOILDEP	(cm)
Cover of exposed rock	ROCKCOV	(%)
Soil characteristics		
Clay content of A-horizon	CLAYA	(%)
Sand content of A-horizon	SANDA	(%)
Clay content of B-horizon	CLAYB	(%)
Sand content of B-horizon	SANDB	(%)
Degree of illuvation from A- to B-horizon	ILLUV%	(%)
Bulk density of each horizon		
Climatic modelling		
Duration of the growth season	GDAYS	(days)
Temperature during growth season	GTEM	(° C)
Temperature during no-growth season	NGTEM	(° C)

5.2.4 DATA ANALYSIS

A multivariate approach to the classification of plant communities was used, involving the two-way indicator species analysis (TWINSPAN) of Hill (1979). Species occurring in a single stand were omitted from the analysis. The TWINSPAN analysis was run using the default options, with the exception that instead of weighting the default cut-levels equally (weight = 1), the default cut-levels were weighted as follows: 0-2% cover was given a weighting of 1, 2-5% cover was given a weighting of 2, and all of the cover interval classes above 5% were given a weighting of 4. This modification of the default cut levels was considered justified as woody elements with a cover greater than 5% were considered far more important than those with a cover between 2 and 5%, while those with a cover less than 2% were considered by far the least important, but still worthy of inclusion in the analysis. This weighting is considered to reflect the perceived importance of cover by woody plants in a way reflected in the literature. If total cover of woody plants is less than 2%, the site would generally be considered grassland; if between 2% and 5%, as grassland by some authors and as wooded grassland by others; if greater than 5% as wooded grassland (cf. Phillips 1971, Pratt & Gwynne 1977, Edwards 1981).

5.3 RESULTS

5.3.1 THE CLASSIFICATION OF VEGETATION UNITS

The classification of stands using the TWINSPAN cluster analysis gave rise to 10 vegetation types (Fig. 5.4) that are considered to represent the range of affinities of wooded patches in the grassland biome. The classification shows relationships between vegetation types, as indicated in the species by stands matrix on which the classification is based (Table 5.2) A problem with the floristic classification is that it does not arrange units in the best way based on structural or functional criteria which were defined *a priori*, namely, based on the biome with which the species has affinity. For example, forest (unit A) and scrub forest (unit B) are separated from each other at the second level of division, and are widely separated in the dendrogram (Fig. 5.4) despite having obvious functional and structural affinity. Similarly, units with fynbos affinity (units F and G) are widely separated in the dendrogram. The

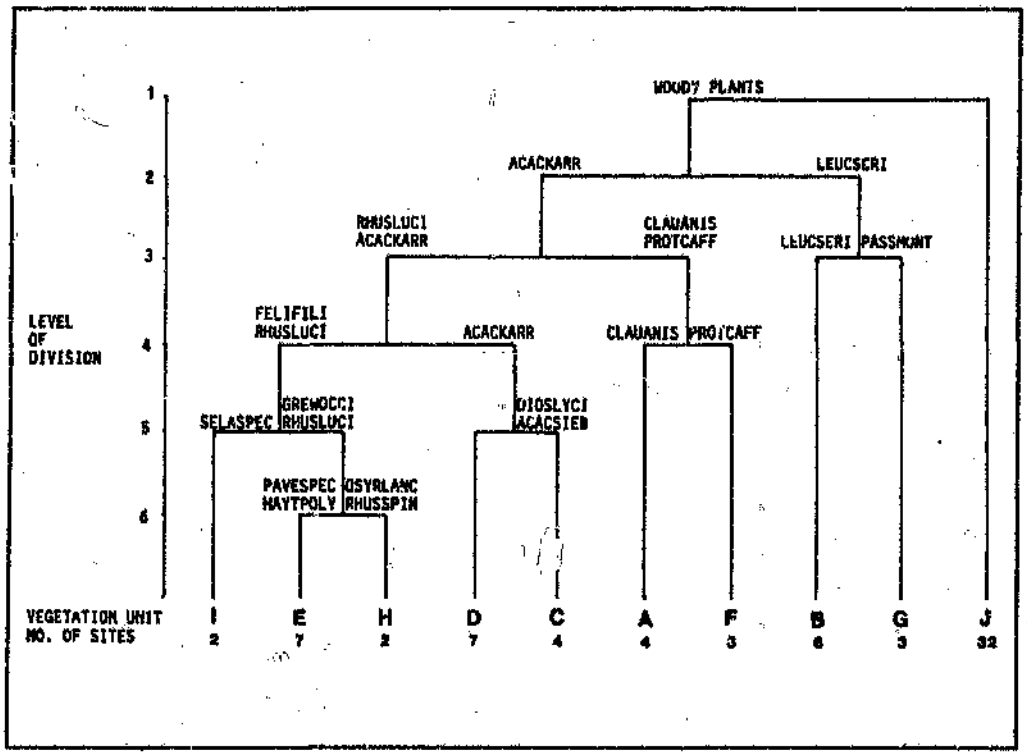


Figure 5.4: Hierarchical classification of stands derived from a TWINSPAN cluster analysis. Indicator species, the final vegetation units (A = forest, B = scrub forest, C = Acacia sieberana/broadleaf savanna, D = A. karoo savanna, E = broadleaf savanna, F = Protea caffra broadleaf sclerophyll, G = Passerina montana ericaceous sclerophyll, H = savanna with karoo elements, I = karoo, J = grassland with <2% cover by woody elements), the number of stands in each unit, and the level of division are indicated for divisions in the dendrogram.

SPECIES	STANDS 22 1111222 22233333323 3313111 112 13417478967825604589562794801230169352	
19 FELI FILI	15---111-11----1--3-----1----------111	000
20 FELI YELL	21-----111------21--------------1-----	000
4 ACAC ATAX	---51--------------------1----------	00100
15 EUCL CRIS	---2111----------1--------1----------	00100
39 RHUS LEPT	--13--------1------------1----------	00100
5 BRAC DISC	----4---------1-----1----------------	001010
6 BUDD SALI	------43------------------------------	001010
16 EUPH SPEC	-----11------------------------------	001010
17 EHRI RIGI	----3-1-----1------------------------	001010
18 EURY SPEC	---------42--------------------------	001010
22 GREW OCCI	---2212-1-111---------1--------------	001010
30 OLEA AFRI	----5-31----1------------------------	001010
31 OSYR LANC	-----111-----------------------------	001010
36 RHUS EROS	-----11------------------------------	001010
37 RHUS LUCI	---1112112--1-2----------------------	001010
41 RHUS SPIN	------122----------------------------	001010
2 ALOE FERO	----------11-------------------------	001011
25 LIPP SPEC	--------1-11------1------------------	001011
43 ZIZI MUCR	---21-------2111----1-----1----------	00110
1 ACAC SIEB	------------------3345----------------	00111
3 ACAC KARR	----1----11353553553-----------------	00111
10 COMB MOLL	--1---------2------------------------	00111
13 DOMB ROTU	----------------1-3---2--------------	0100
38 RHUS MACK	--------------------11-2-------------	0100
33 PROT CAFF	-------------------------533---------	010100
7 CANT CILI	----------------------1-1--1----------	010101
8 CANT INER	----------1----------3-5------------	010101
9 CLAU ANIS	----------------------22-4------------	010101
23 HETE ARBO	------1--------------51--------------	010101
24 HALL LUCI	----------------------5----1----------	010101
11 CUSS PANI	----1-1----------2--3---1----------	01011
29 MAYT POLY	--2-1--------------------------------	01011
32 PAVE SPEC	--2-1--------------------------------	01011
12 DIOS LYCI	--2---1----------3111-244-111-1------	011
28 MAYT HETE	---211-1----1-1---2---55----111-------	011
14 DIOS WEYT	-----1---1-2----------4----1-2-1------	10
35 RHUS DENT	-----1-----1------11--5-3--12-211-1---	10
27 MYRS AFRI	-----1--------------1-2-----2---1-3--	1100
21 GNID HAIR	------------------------------------12	1101
34 PASS MONT	----------------------------------434	1101
42 SELA SPEC	11----------------------------------12	1101
26 LEUC SERI	----------------------------5543422--	111
40 RHUS PYRO	-----1----------------------4--------	111
	00000000000000000000000000111111111	
	00000000000000000000011111110000111	
	00000000000111111111110001110111111	
	00111111111000000000110011 01111	

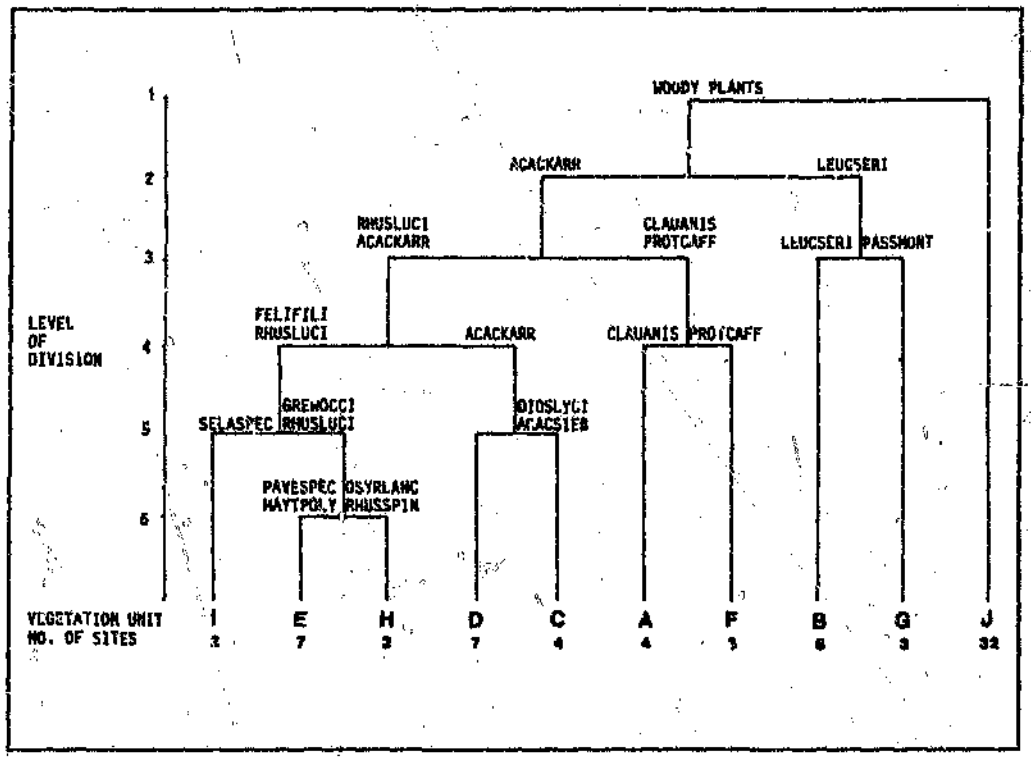


Figure 5.4: Hierarchical classification of stands derived from a TWINSPAN cluster analysis. Indicator species, the final vegetation units (A = forest, B = scrub forest, C = Acacia sieberana/broadleaf savanna, D = A. karoo savanna, E = broadleaf savanna, F = Protea caffra broadleaf sclerophyll, G = Passerina montana ericaceous sclerophyll, H = savanna with karoo elements, I = karoo, J = grassland with <2% cover by woody elements), the number of stands in each unit, and the level of division are indicated for divisions in the dendrogram.

Table 5.2: The species by stands matrix and basis for division of vegetation units as identified in the TWINSPAN cluster analysis. Species numbers and abbreviations are provided; the names are given in APPENDIX 2. Stand numbers are written vertically, the first two stands being numbers 21 and 23. The values in the matrix correspond to the cover intervals in the default option of TWINSPAN, with values 1 to 5 indicating cover intervals (%) of >0-2, >2-5, >5-10, >10-20 and >20 respectively. The columns of values on the right and on the bottom of the matrix indicate divisions of species and stands respectively at successive levels of division in the cluster analysis.

SPECIES	STANDS 22 1111222 22233333323 3313111 112 13417478967825604589562794801230169352	
19 FELI FILI	15---111-11----1--3-----1---------111	000
20 FELI YELL	21-----111------21-------------1----	000
4 ACAC ATAX	---51-------------------1----------	00100
15 EUCL CRIS	---2111----------1-------1----------	00100
39 RHUS LEPT	--13--------1-----------1----------	00100
5 BRAC DISC	----4---------1-----1----------------	001010
6 BUDD SALI	------43-----------------------------	001010
16 EUPH SPEC	-----11------------------------------	001010
17 EHRI RIGI	----3-1-----1------------------------	001010
18 EURY SPEC	---------42--------------------------	001010
22 GREW OCCI	---2212-1-111---------1--------------	001010
30 OLEA AFRI	----5-31----1------------------------	001010
31 OSYR LANC	-----111-----------------------------	001010
36 RHUS EROS	-----11------------------------------	001010
37 RHUS LUCI	---1112112--1-2----------------------	001010
41 RHUS SPIN	------122----------------------------	001010
2 ALOE FERO	----------11-------------------------	001011
25 LIPP SPEC	---------1-11------1-----------------	001011
43 ZIZI MUCR	---21-------2111----1-----1----------	00110
1 ACAC SIEB	----------------3345-----------------	00111
3 ACAC KARR	----1----11353553553-----------------	00111
10 COMB MOLL	--1---------2------------------------	00111
13 DOMB ROTU	----------------1-3---2--------------	0100
38 RHUS MACK	--------------------11-2-------------	0100
33 PROT CAFF	-------------------------533---------	010100
7 CANT CILI	---------------------1-1--1----------	010101
8 CANT INER	----------1----------3-5-------------	010101
9 CLAU ANIS	----------------------22-4------------	010101
23 HETE ARBO	------1---------------51--------------	010101
24 HALL LUCI	----------------------5----1----------	010101
11 CUSS PANI	----1-1----------2--3---1----------	01011
29 MAYT POLY	--2-1--------------------------------	01011
32 PAVE SPEC	--2-1--------------------------------	01011
12 DIOS LYCI	--2---1----------3111-244-111-1------	011
28 MAYT HETE	---211-1----1-1---2---55----111-------	011
14 DIOS WEYT	-----1---1-2---------4----1-2-1------	10
35 RHUS DENT	-----1-----1------11--5-3--12-211-1---	10
27 MYRS AFRI	-----1---------------1-2----2---1-3--	1100
21 GNID HAIR	------------------------------------12	1101
34 PASS MONT	----------------------------------434	1101
42 SELA SPEC	11-------------------------------12	1101
26 LEUC SERI	----------------------5543422--	111
40 RHUS PYRO	-----1-----------------4--------	111
	00000000000000000000000000111111111	
	00000000000000000000011111110000111	
	00000000001111111111100001101111	
	00111111111000000000110011 01111	

most appropriate arrangement is indicated by the choice of labels for naming vegetation units (A to J, Fig. 5.4).

The affinity, and selected environmental conditions of each site, are summarised in Table 5.3.

The first vegetation type identified in the classification was that with woody elements absent or present at extremely low cover (<2%), namely unit J (Fig. 5.4). The dichotomy at the second level of division was indicated by Leucosidea sericea[2] (LEUCSERI)[3] on the one hand, and Acacia karroo (ACACKARR) on the other. The group on the right of this dichotomy was divided again in the analysis, based on the indicator Passerina montana (PASSMONT) on the one hand, giving rise to ericaceous sclerophyll (unit G), and Leucosidea sericea (LEUCSERI) on the other, giving rise to scrub forest (unit B). The group indicated by A. karroo at the second level of division was divided at the next level based on the indicator species A. karroo and Rhus lucida (RHUSLUCI) in the negative group, and Protea caffra (PROTCAFF) and Clausenia anisata (CLAUANIS) in the positive group. The positive group was divided further on the basis of the latter two species being indicators of positive and negative groups respectively, giving rise to P. caffra broadleaf sclerophyll (unit F) and forest (unit A) respectively. The group indicated by A. karroo and R. lucida at the third level of the division was divided at the fourth level based on the indicator species A. karroo with cover greater than 5% in the positive group and with cover less than 5% in the negative group, and Felicia filifolius (FELIFILI) and R. lucida in the negative group. The positive group was divided further based on the indicator species A. sieberana (ACACSIEB) and Diospyros lycioides (DIOSLYCI), both in the positive group. This division gives rise to two vegetation units, one an A. karroo savanna (unit D), the other an A. sieberana savanna with broadleaf elements (unit C). The negative group at the fourth level of division (indicated by F. filifolius and R. lucida) was divided further, the negative group indicated by Selago sp. (SELASPEC), giving rise to the unit of karoo (unit I), the positive group indicated by Grewia occidentalis (GREWOCCI) and R. lucida. This group was divided again based on the

---

[2] Species nomenclature follows Gibbs Russel et al. (1987).

[3] Species names and abbreviations are given in APPENDIX 2.

Table 5.3: Selected environmental conditions associated with each site (STE) visited in the study, including the duration of the growth season (GDAYS), growth season temperature (GTEM), soil depth (DEP), clay content of A- and B-horizons (CA, CB), sand contents of these horizons (SA, SB), increase in clay content from the A- to B-horizons (ILLUV), cover by exposed rock (RK), slope (SL), evenness of the soil surface (SDSL), aspect (AS), fire frequency (F) and grazing intensity (G). Tree cover (TREE) is also provided, as is the site number (NO) and vegetation unit into which it was classified (T).

STE	NO	T	GDAYS	GTEM	DEP	CA	SA	CB	SB	ILLUV	RK	SL	SDSL	AS	F	G	TREE
P1	1	E	74.9	19.2	15	42	35	42	34	0.1	19	15	0.14	SE	1	2	46.2
P2	2	D	61.6	19.8	70	32	50	44	41	-12.7	2	5	0.11	NW	1	4	26.8
P3	3	J	57.5	19.9	20	26	55	26	55	0.2	10	5	0.04	NW	2	4	0.5
P4	4	J	68.5	19.5	80	20	73	24	69	5.1	1	4	0.03	SE	2	4	1.7
P5	5	E	79.5	19.5	20	27	62	27	61	0.2	45	7	0.29	NW	1	1	10.3
P6	6	D	61.0	19.2	85	21	73	25	70	1.6	1	4	0.03	NW	1	5	9.6
P7	7	D	62.0	19.4	130	47	30	50	33	2.5	0	0	0.02	0	2	4	60.2
P8	8	J	57.5	19.9	25	33	54	37	48	4.1	0	4	0.03	SE	2	3	0.5
P9	9	E	61.6	19.6	10	55	24	56	23	0.9	33	15	0.19	S	1	2	91.8
P10	10	F	69.6	19.2	10	26	65	26	64	0	17	9	0.08	S	2	3	41.3
V1	11	J	85.0	17.3	70	39	47	46	41	7.4	0	9	0.02	N	4	3	1.6
V2	12	B	95.0	16.8	40	52	22	60	19	7.9	30	30	0.18	N	3	3	3.4
V3	13	B	95.4	17.1	35	49	26	62	19	12.7	23	28	0.25	N	3	4	15.3
V4	14	B	101.7	16.1	40	50	21	55	19	4.7	12	34	0.16	S	4	3	8.8
V5	15	B	101.4	15.8	70	57	10	60	6	3.8	0	25	0.11	S	1	2	48.2
V6	16	J	86.9	17.3	10	59	10	60	9	0.8	2	2	0.07	0	3	4	0.5
V7	17	J	86.9	17.3	65	49	19	61	17	-11.7	0	6	0.05	S	3	4	0.5
V8	18	J	101.4	16.0	60	49	24	53	23	3.9	0	13	0.03	W	3	3	0.5
B1	19	G	86.1	16.5	50	17	47	23	52	5.8	5	23	0.21	NE	2	1	24.1
B2	20	E	91.5	16.6	40	21	57	23	59	2.1	9	22	0.10	N	1	2	4.2
B3	21	J	74.4	16.9	65	22	50	32	44	9.8	0	8	0.05	N	2	2	0.5
B4	22	J	88.9	16.8	130	22	65	30	58	7.8	0	8	0.03	E	2	4	0.5
B5	23	G	80.2	16.2	50	20	68	22	68	1.8	0	6	0.04	W	2	4	7.8
B6	24	B	85.9	15.8	110	28	50	40	44	11.9	2	14	0.09	S	2	4	10.2
B7	25	J	74.4	16.9	110	30	42	44	37	13.8	0	7	0.03	S	2	4	0.5
B8	26	J	99.0	16	120	24	64	36	50	12	12	10	0.09	S	2	3	0.5
BL1	27	E	63.9	17.8	30	33	49	26	58	-7.1	21	32	0.14	S	1	4	28.4
BL2	28	E	60.6	17.9	15	40	41	41	40	0.9	10	3	0.05	0	1	4	13.7
BL3	29	J	55.0	18.4	110	44	35	60	23	16.5	0	2	0.03	0	2	4	0.5
BL4	30	E	58.9	18.7	35	39	42	38	47	-1.8	42	28	0.21	N	2	4	3.5
BL5	31	J	61.2	18.8	75	40	52	56	34	15.8	0	3	0.03	0	1	2	0.5
BL6	32	J	55.0	18.4	33	31	54	34	52	3.1	0	3	0.03	0	2	3	0.5
BL7	33	D	60.6	17.7	110	34	47	45	40	11.1	0	2	0.03	0	2	4	41.4
BL8	34	J	55.0	18.4	130	16	80	32	63	16.2	0	3	0.04	0	1	1	0.5
BL9	35	J	61.2	18.8	45	23	69	34	60	10.9	0	1	0.02	0	1	3	0.5

Table 5.3 (cont.)

STE	NO	T	GDAYS	GTEM	DSP	CA	SA	CS	SB	ILLUV	RK	SL	SDSL	AS	F	G	TREE
M1	36	J	66.3	13.7	60	34	34	50	24	16	0	3	0.03	O	1	3	0.5
M2	37	I	79.0	12.2	40	22	40	28	40	6.1	22	24	0.22	S	2	2	6.5
M3	38	G	63.6	13.4	35	22	56	48	37	25.6	3	5	0.04	W	2	3	18.4
M4	39	J	72.4	13.3	60	24	47	61	22	37.2	0	3	0.03	O	1	2	0.5
M5	40	I	68.1	13.2	55	38	25	63	9	25.8	19	21	0.08	N	1	2	23.6
M6	41	J	72.4	13.3	55	24	50	53	35	29.2	0	2	0.02	O	1	2	0.5
Q1	42	D	52.9	17.6	90	20	60	38	47	17.4	0	1	0.02	O	1	3	9.6
Q2	43	J	49.1	18.4	45	28	62	74	18	46.4	0	1	0.0?	O	1	3	0.5
Q3	44	D	57.5	18.1	70	36	40	61	24	25	0	4	0.04	N	2	2	20.3
Q4	45	J	57.2	18.6	25	31	49	36	46	4.8	0	4	0.03	N	2	2	0.5
Q5	46	H	68.1	17.1	47	44	23	74	1	30.3	28	25	0.14	S	1	5	23.8
Q6	47	H	68.1	17.3	45	38	33	46	26	7.8	28	23	0.15	S	1	4	6.5
Q7	48	D	52.8	18.2	60	56	20	70	10	14.3	34	18	0.12	N	2	3	11.9
Q8	49	J	51.2	18.4	30	41	27	79	9	37.5	28	9	0.09	N	2	3	0.5
Q9	50	J	51.2	18.4	105	39	31	65	15	26.4	0	4	0.02	N	2	3	0.5
K1	51	J	114.0	16.2	25	56	12	57	10	1.5	11	10	0.06	E	4	3	0.5
K2	52	A	102.0	16.5	30	48	30	51	17	3.2	80	3	0.29	O	1	1	30.7
K3	53	J	96.6	17	115	66	2	69	16	3	0	6	0.03	N	3	2	0.5
K4	54	F	98.3	17.0	25	58	19	58	21	0.1	51	19	0.17	N	4	1	7.1
K5	55	F	110.0	16.2	30	63	8	67	6	4.5	40	15	0.12	S	4	1	7.7
K6	56	A	110.6	15.9	30	57	8	59	5	2.4	8	44	0.37	S	1	1	150
K7	57	B	114.0	16.2	40	60	11	68	6	8.1	4	13	0.04	E	2	1	56.9
H1	58	J	105.2	18.5	50	46	38	50	35	4.1	0	8	0.05	SE	3	1	0.5
H2	59	A	116.2	17.7	50	39	43	59	23	19.5	23	40	0.31	S	1	1	186
H3	60	C	115.3	17.9	80	49	37	54	32	4.5	13	37	0.23	SW	3	2	30.4
H4	61	C	115.0	18.1	100	50	33	68	14	18.4	14	10	0.11	S	3	2	27.7
H5	62	J	105.2	18.5	30	57	15	65	10	7.4	0	8	0.04	N	3	3	0.5
H6	63	J	105.2	18.5	100	65	14	76	1	11.8	0	2	0.03	O	4	1	0.5
VR1	64	J	115.7	19.3	100	61	7	62	13	-11.5	0	4	0.02	SE	3	2	0.5
VR2	65	A	128.3	18.6	50	56	14	74	2	17.4	34	30	0.16	S	1	1	75.9
VR3	66	C	126.6	18.8	70	32	50	36	47	4.2	14	34	0.25	W	3	4	47.1
VR4	67	D	120.5	18.9	100	26	65	32	60	6	0	7	0.05	W	3	4	11.7
VR5	68	J	115.7	19.3	70	22	66	23	63	-8.8	0	3	0.02	O	3	3	0.5
VR6	69	J	115.7	19.3	110	49	35	63	27	14.1	0	3	0.02	O	3	3	0.5
VR7	70	J	115.7	19.3	45	30	62	30	63	0.1	0	2	0.03	O	2	5	0.5

indicator species Pavetta sp (PAVESPEC) and Maytenus polyacantha (MAYTPOLY) in the negative group, and Osyris lanceolata (OSYRLANC) and Rhus longispina (RHUSSPIN) in the positive group. These correspond to a broadleaf savanna (unit E) and savanna with karoo elements (unit H) respectively.

5.3.2 THE DISTRIBUTION OF WOODED PATCHES IN THE GRASSLAND BIOME

5.3.2.1 CLIMATE

The distribution of wooded patches in the grassland biome is not determined by microclimatic conditions that distinguish them from the macroclimate of the biome itself. This is illustrated by the occurrence of all of the wooded patches within the region of the no-growth temperature - duration of the growth season plane that discriminates grasslands from other summer rainfall biomes (Fig. 5.5). Either climatic conditions identified at the subcontinental scale as determining the distribution of the grassland biome do not apply at the local scale, or the significance of these conditions has not been properly established.

An upper limit to the abundance (estimated on the basis of aerial cover) of woody elements appears to be determined in a general way by a combination of the duration of the growth season and by the temperature during the growth season (Fig. 5.6). An increase in either the duration of the growth season or the wet season temperature results in an increase in the upper limit of cover by woody plants, reflecting an increase in site favourability. Despite this general relationship between maximum cover and climate, grasslands without any woody elements occur over the entire range of climatic conditions covered in the study.

5.3.2.2 SOILS

The relationship between soil types and the occurrence of wooded and non-wooded

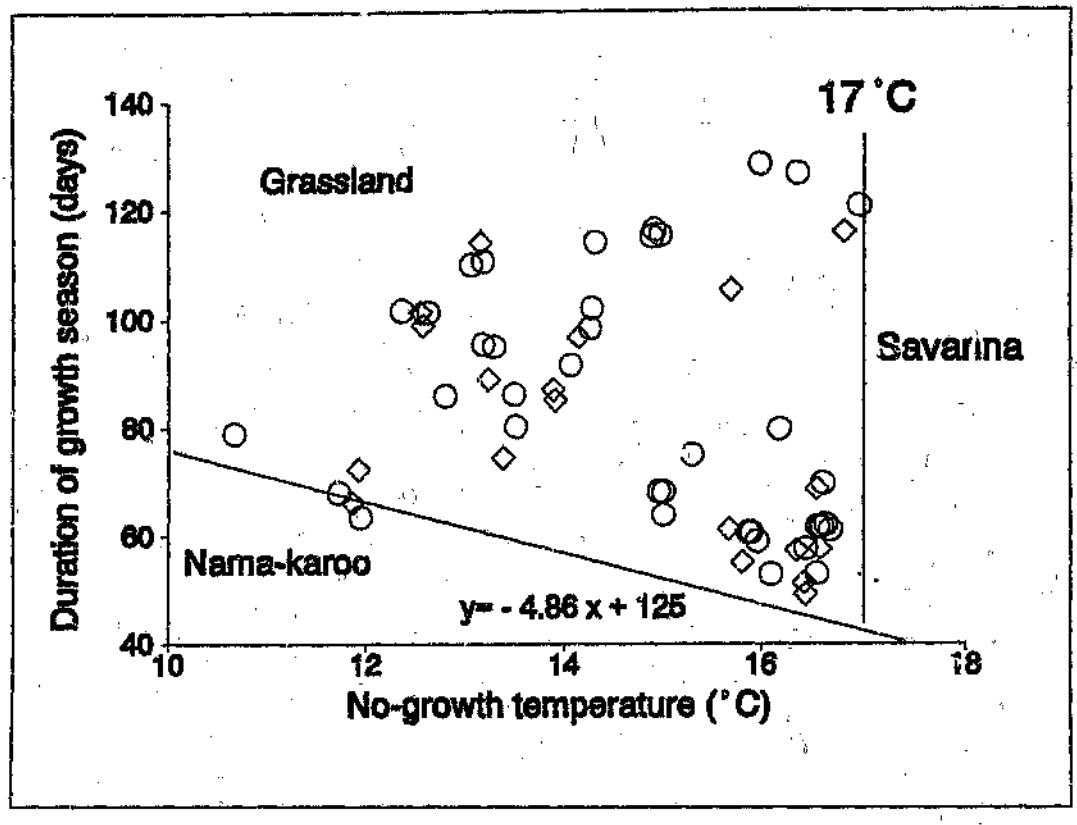


Figure 5.5: The distribution of study sites in the grassland biome with (○) and without (◇) woody plants in relation to the duration of the growth season and the temperature during the no-growth season. The most important aspects of microclimate have been included for the study sites. The names of biomes are given based on the subcontinental scale analysis of the distribution of the summer rainfall biomes in relation to macroclimate.

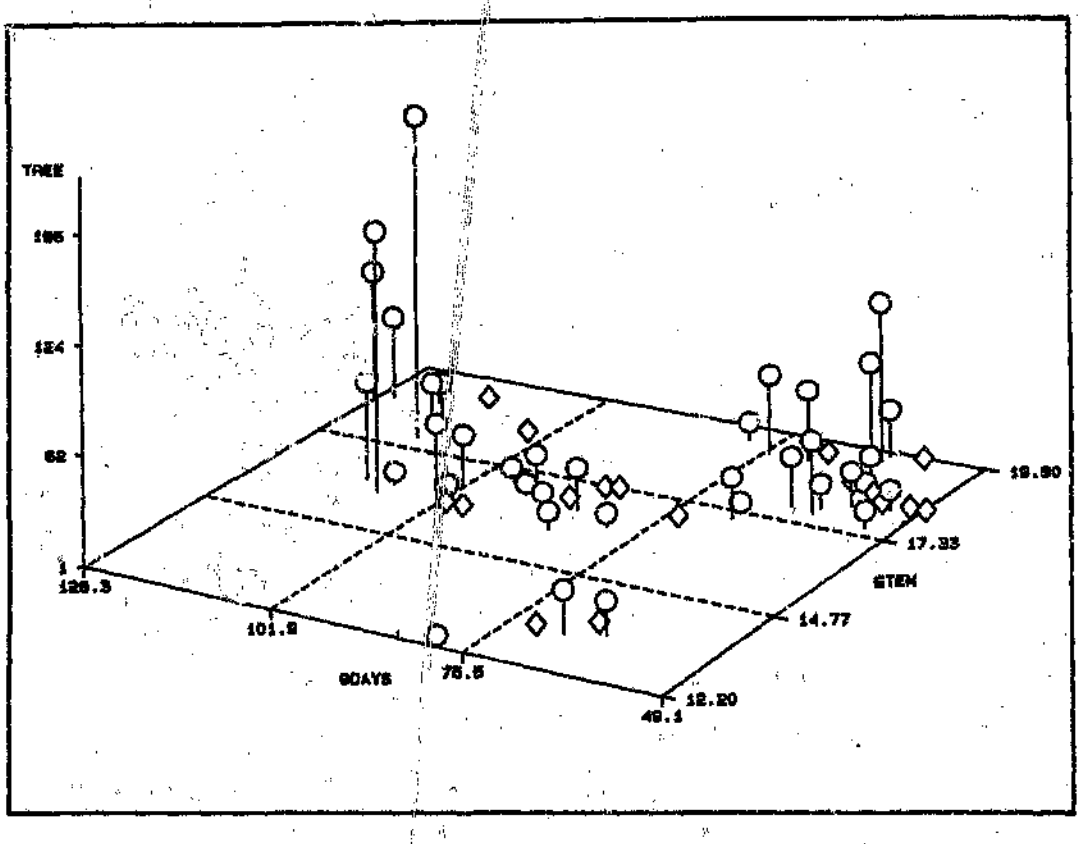


Figure 5.6: The distribution of study sites in the grassland biome with (○) and without (◇) woody plants in relation to the duration of the growth season (GDAYS) and the temperature during the growth season (GTEM). The total cover (%) of woody plants (TREE) is given on the vertical axis.

patches is indicated in Table 5.4. Sites with a well developed illuvial B-horizon[4] (including duplex soils, vertisols and soils which showed evidence of waterlogging) generally supported grasslands with less than 2% cover by woody elements. A total of eight sites out of 29 characterised by soils belonging to these types supported woody elements. The occurrence of woody plants in these sites could largely be attributed to the exclusion of fire or other anthropogenic factors such as a history of heavy grazing (sites B6, BL7, H4, P2, P6, Q1, Q3, VR4; Table 5.5). In addition, sites were dominated by one or a combination of Acacia karroo, A. sieberana and Leucosidea sericea, all of which are considered to be invading the grassland biome extensively (Trollope 1974, Coates Palgrave 1977, Aucamp et al. 1983, Friedel 1987). It is possible that in an undisturbed situation these sites may have supported grassland.

The separation of soils with a shallow hardpan horizon or with shallow impervious rocks and those with a lithocutanic B-horizon (Table 5.4) is based on the extent to which the B-horizon was characterised by weathering rock. Where absent, the soil was considered to have shallow impervious rock, and to be similar from the point of view of the plant to a soil with an indurated B-horizon. Where present, the site was considered to have a lithocutanic B-horizon. Of 11 sites with shallow impervious rock, only one supported woody elements with cover greater than 2% (Table 5.4). This site was on cave sandstone, with a shallow, sandy A-horizon, and supporting Passerina montana of fynbos affinity (site B5; Table 5.5). It was in a situation that was protected from fire, being on an island of soil approximately 0.5 ha in size, and

---

[4] A well developed illuvial B-horizon is defined here as one in which the B-horizon is fully developed to a depth of greater than 50cm (excluding lithocutanic B-horizons, or those of stratified alluvium or regic sands), and which shows an increase in the clay content from the A- to the B-horizon. This differs from more conventional definitions, in which a specific increase in clay content over a specified depth is stipulated (cf. Soil Survey Staff 1960, MacVicar et al. 1977). In order to investigate the hypothesis of Feely (1987) that the presence of a 'well developed cutanic B-horizon' limits the establishment of woody plants, as broad a definition as possible of a 'cutanic B-horizon' has been taken. He neither defined a 'cutanic B-horizon', nor did he quantify soil texture in his study. The basis for his interpretation of a cutanic B-horizon is not clear, but was probably based on landscape features and topography rather than soil texture *per se*.

TABLE 5.4: The occurrence of sites with woody cover greater and less than 2% within the grassland biome, in relation to 3 broad categories of soil type; those with a well developed illuvial B-horizon (sensu Feely 1987), those with a shallow hardpan horizon or with shallow impervious rock, and lithocutanic soils with a poorly developed illuvial B-horizon.

	Well developed illuvial B-horizon (including duplex, vertic or waterlogged)	Shallow hardpan or shallow impervious rocks	Poorly developed illuvial B-horizon (lithocutanic soils)
> 2% woody cover	8	1	29
< 2% woody cover	21	10	1

TABLE 5.5: An analysis of stands that may be considered exceptions to the generally observed relationships between soils and the occurrence of woody elements.

SITE	DESCRIPTION OF SOIL	DESCRIPTION OF VEGETATION	OTHER COMMENTS
WELL DEVELOPED ILLUVIAL B-HORIZON (INCLUDING DUPLEX, VERTIC OR WATERLOGGED SOILS) (n=8)			
B6	Neocutanic B-horizon	Leucosidea sericea scrub forest	Protected from fire, history of heavy grazing
BL7 & P6	Red structured B-horizon	Acacia karoo savanna	History of heavy grazing
H4	Waterlogged	Acacia sieberana savanna	Protected from fire
P2, Q1 & Q3	Duplex soil with degraded A-horizon	Acacia karoo savanna	History of heavy grazing
VR4	Yellow-brown apedal B-hoizon	Acacia sieberana savanna with A. karoo	History of heavy grazing
SHALLOW HARDPAN OR SHALLOW IMPERVIOUS ROCKS (n=1)			
B5	Cave sandstone (depth = 0.7m)	Passerina montana fynbos community	Protected from fire
POORLY DEVELOPED ILLUVIAL B-HORIZON (n=1)			
Q8	Lithocutanic B-horizon	Grassland	Cleared by hand for stock, burned frequently

completely surrounded by exposed rock (cave sandstone).

In contrast, of 30 sites with soils with a poorly developed illuvial B-horizon (shallow lithocutanic B-horizon or unconsolidated alluvium), but which also did not have a shallow impervious rock layer, 29 had woody elements (Table 5.4). The site without woody elements had been cleared by hand for stock, a condition that had been maintained by frequent burning (site Q8; Table 5.5).

The sites with a well developed illuvial B-horizon were divided into three classes on the basis of the maximum difference in the absolute clay content between the A- and B-horizons; those with an increase of less than 5%, 5-15% and greater than 15%. These data show little relationship between the degree of illuviation and the ability of a site to support woody elements (Table 5.6), a relationship that may be expected if the degree of illuviation *per se* affected the occurrence of woody elements, as suggested by Feely (1987).

5.3.2.3 TOPOGRAPHY AND FIRE

It seems unlikely that the observed correlation between the presence of a well developed cutanic B-horizon and the distribution of grasslands reported by Feely (1987) is causal. Rather, these soil types are associated with landscape positions subjected to frequent, intense fires. They occur on gentle, even slopes and are not associated with outcrops of parent rocks (Table 5.7). In contrast, shallow lithocutanic soils generally occur on steeper, more uneven slopes, and have greater rock exposure than any of the other soil types identified in the present study. Steep slopes, particularly with a leeward aspect, uneven surface characteristics, or the occurrence of rocky outcrops at a site, would reduce plant density, fuel load, and therefore fire frequency and intensity (Everson et al. 1988).

For a given growth season duration, grassland occurs in situations of low slope compared to wooded sites (Fig. 5.7). Aspect is also important in determining the degree of woodiness, generally with southern aspect slopes better wooded than other aspects for a given duration of growth season and slope (Fig. 5.7). On less steep slopes the effect of aspect is less marked than on steeper slopes. The inclusion of

TABLE 5.6: The occurrence of wooded patches within the grassland biome in situations with an illuvial B-horizon, but with different (absolute) percentage increases in the clay content from the A- to the B-horizons.

	Increase in clay content (%)		
	0-5	5-15	>15
< 2% woody cover	1	4	3
> 2% woody cover	6	7	8

TABLE 5.7: Relationships between soil characteristics and topographical characteristics that influence fire frequency and intensity.

	Well developed illuvial B-horizon including duplex or waterlogged soils (n=29)	Shallow hardpan or shallow impervious rocks (n=11)	Poorly developed illuvial B-horizon	
			Lithocutanic B-horizon (n=29)	Unconsolidated B-horizon (n=1)
SLOPE (degrees)				
0-5	18	7	3	1
6-10	9	4	3	
11-15	2		4	
16-20			2	
21-30			10	
31-40			6	
>40			1	
SLOPE VARIATION (sd units)				
0-.05	25	9	3	1
.06-.10	3	2	4	
.11-.15	1		7	
.16-.20			5	
.21-.30			8	
>.30			2	
ROCKINESS (% cover)				
0-5	27	9	1	1
6-10		1	4	
11-15	2*	1	5	
16-20			3	
21-30			8	
31-40			4	
>40			4	

* Transported from upslope.

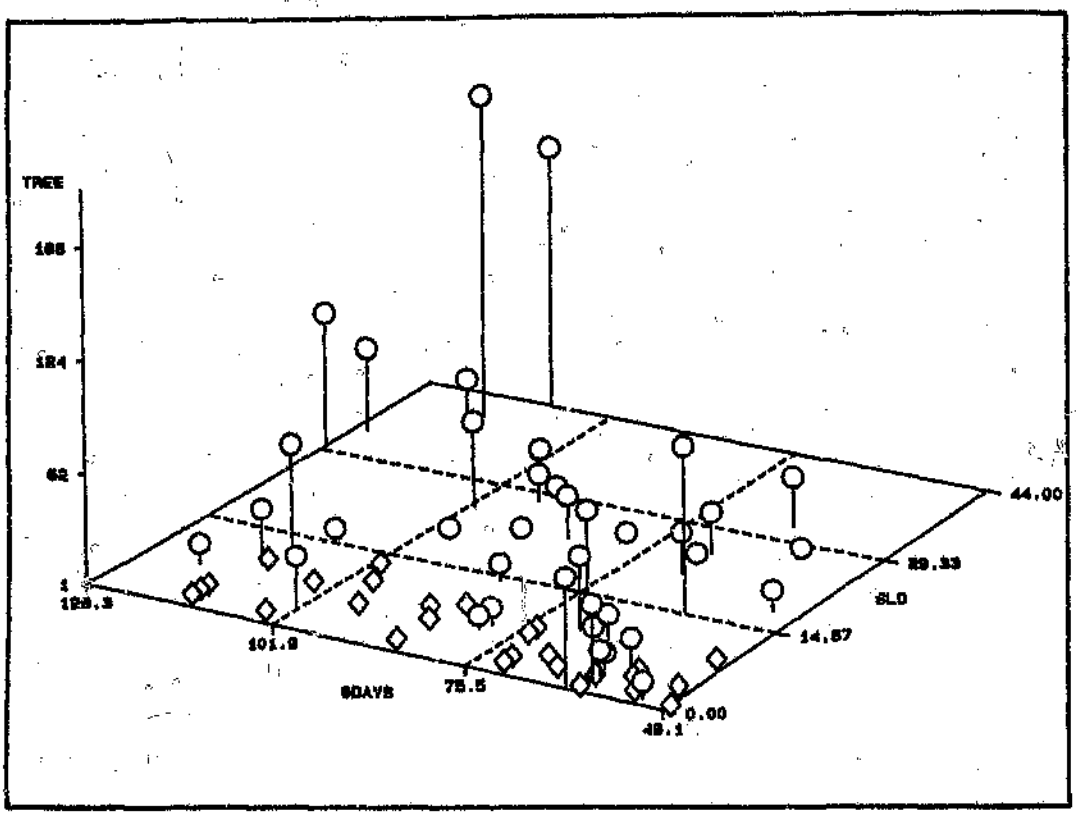


Figure 5.7: The distribution of study sites in the grassland biome with (○) and without (◇) woody plants in relation to the duration of the growth season (GDAYS) and slope (SLO). The total cover (%) of woody plants (TREE) is given on the vertical axis.

slope and aspect in the water balance component of the study suggests that it is an effect of slope and aspect other than on the moisture balance and temperature regime that affects site woodiness. The only other factor that is suggested to be important is the effect of these two factors on the fire regime in relation to prevailing winds. The prevailing winds in the grassland biome during the dry season are predominantly southerly to south-easterly (Jackson 1952, Tyson 1969), with southern and south-eastern slopes generally subject to less frequent and intense fires than northern and north-eastern slopes (Everson et al. 1988).

Some of the best known fire exclosure sites in the grassland biome are located at Thabamhlope (Fig. 5.1), where fire has been excluded for about 50 years (W. Trollope, personal communication). One site has soils with a well developed illuvial B-horizon. The site supports dense scrub forest (Fig. 5.8), suggesting that under the climatic conditions at Thabamhlope at least, fire and not soil characteristics, is the most important factor preventing the establishment of woody plants.

5.4 DISCUSSION

This section of the study has shown that topography, soils, grazing and fire are important determinants of the distribution of woody elements in the grassland biome. It will be argued that the features of climate associated with the grassland biome promote frequent fire, and thereby determine the distribution of the grassland biome as a whole.

5.4.1 WHY NOT TEMPERATURE ALONE?

Cool temperatures during the non-growth season have frequently been cited as a cause of the absence of woody elements from the grassland biome (Acocks 1975, Rutherford & Westfall 1986, Ellery et al. '991). The presence of woody plants in areas of the grassland biome that experience the coldest dry season temperatures in South Africa suggests that it is not temperature alone that limits the establishment of woody plants. The coldest winter temperature ever recorded in South Africa was measured on the farm Buffelsfontein between Molteno and Dordrecht in the eastern Cape during the winter of 1991. Some of the sites visited at Marshmoor in the

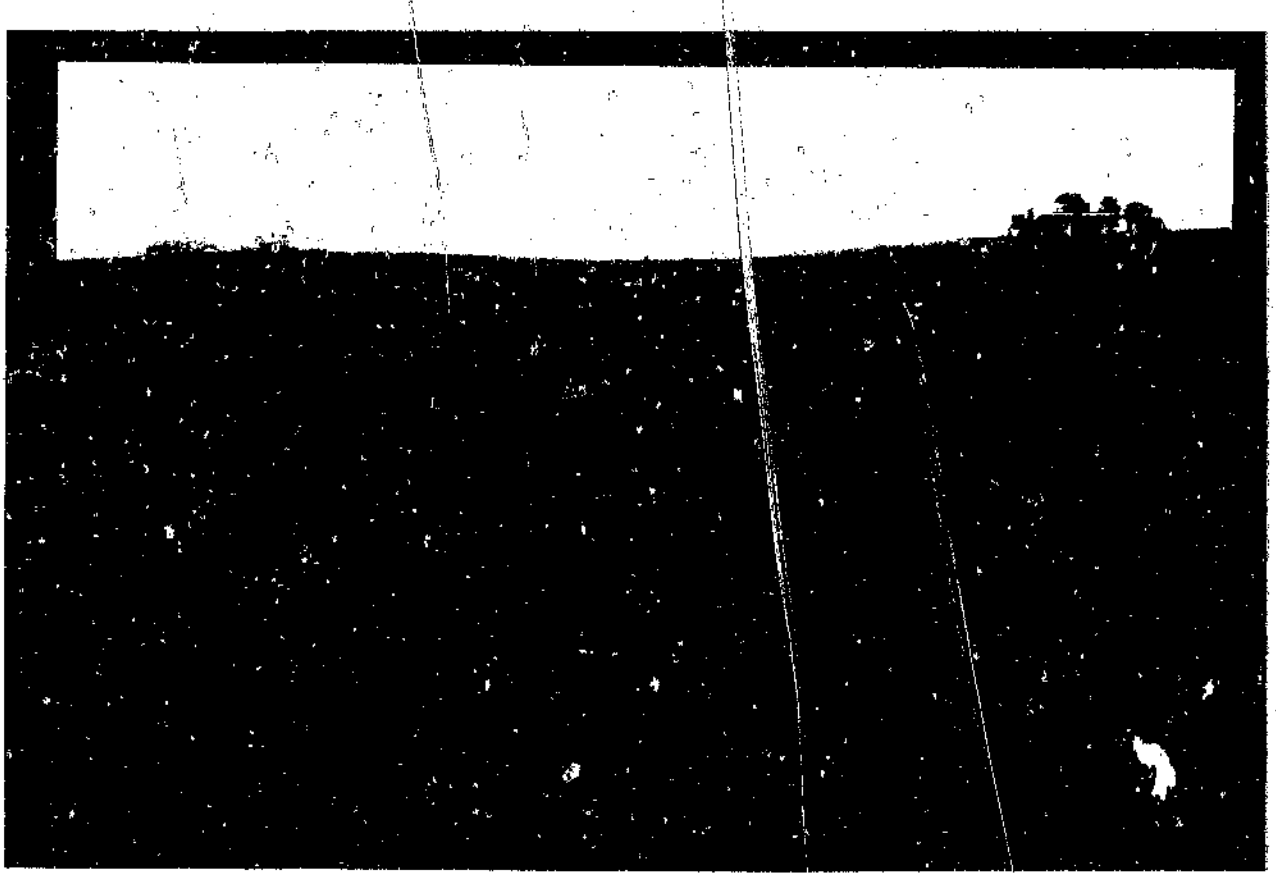


Figure 5.8: The fire exclosure at Thabamhlope in Natal. The area where fire was not excluded is grassland. The area of exclusion has become a dense scrub-forest.

present study (Fig. 5.1) were situated within 10km of this station, all at a similar altitude and experiencing similar temperature and moisture conditions (Weather Bureau 1988). A number of these sites supported woody elements, their distribution pattern being determined by landscape features identical to those at sites elsewhere in the grassland biome. It seems likely that even the sites that support woody elements in the vicinity of Marshmoor experience temperatures colder than elsewhere in the biome that do not support woody elements.

A further source of evidence suggesting that temperature is not the major determinant of the presence or absence of woody elements at a site is presence of woody elements in topographic positions that are not protected from cold winter temperatures or frost. Of the sites dominated by A. karroo, many were on extremely shallow slopes in situations that are not protected from frost or cold winter temperatures. Stands dominated by this species have been observed to survive extreme frosts. With these observations in mind a more appropriate question is 'why is A. karroo not more widespread in the grassland biome?'

Woody plants in other parts of the world are able to withstand the effects of freezing temperatures. Adaptations to low temperature include supercooling, extracellular freezing and extraorgan freezing (Arris & Eagleson 1989). Whether or not any southern African woody plant species are able to withstand freezing temperatures by one or other of these mechanisms has not yet been established. The presence of woody plants in areas that experience extremely cold dry season temperatures suggests that there are. These include the woody elements of Afromontane affinity in the Highlands of Lesotho, the woody plants of the nama-karoo biome (previous chapter) and the presence of woody elements in the coldest region of the grassland biome of South Africa. Areas in which these plants are found are not particularly cold by global standards.

5.4.2 A RE-EVALUATION OF THE IMPORTANCE OF CLIMATE IN DETERMINING THE DISTRIBUTION OF SOUTH AFRICA'S GRASSLANDS

The climate of the grassland biome is characterised by a moderate to high rainfall during the warm season, and a relatively cool dry season. It has been suggested that

this combination of climatic features intrinsically favours frequent fires (Stephenson 1990, Ellery et al. 1991). Net primary production is sufficiently high during the wet season to allow the accumulation of abundant fuel, and the seasonal drought allows the vegetation to dry out, ignite and carry fire. The effect of fire in restricting the distribution of woody elements has been recognised widely, and frequent burning is considered to favour the grassland habit (Vogl 1974, Axelrod 1985, Sims 1988).

In areas with a prolonged dry season it appears almost impossible to protect vegetation against man-made fires (Dimbleby 1977). The same probably applies to natural fires, given an ignition source. Of South Africa's biomes, the grassland biome has the highest lightning density (Manry & Knight 1986), a feature likely to promote frequent burning, even before the continent was inhabited by humans that lit fires at will.

Within this 'fire prone environment' sites protected from fire, or those that are subjected to fires of low intensity, are susceptible to encroachment by woody plants. Grazing is a major determinant of the spatial and temporal dynamics of fuel, and therefore of the ability of vegetation to carry fire (Anderson 1982). The interaction of topography and wind also affects the distribution of woody plants. Steep leeward slopes are protected from fire, and they are prone to encroachment by woody plants. The occurrence of 'berg' winds [5] over the eastern seaboard dessicates vegetation and renders it susceptible to burning. Forest patches of the eastern seaboard are confined to 'berg wind shadow areas' (van Daalen & Geldenhuys 1988), illustrating the interactions of wind, topography and fire. Berg winds are sometimes preceded or terminated with the passage of a cold front (Tyson 1969). This combination of circumstances must render vegetation extremely susceptible to fire effects.

A further fire-promoting feature of climate in South Africa's grassland biome is frost. The occurrence of frost *per se* in the grassland biome has been considered to limit the establishment of woody elements (Acocks 1975), and would appear to be correlated

[5] *Berg winds* are hot, dry winds that occur as a result of the subsidence of air from above the escarpment to the coast in the transition zone between anticyclonic and cyclonic circulations in winter (Tyson 1969).

to both the present dry season temperature index (no-growth temperature) as well as the mimimum temperature of the coldest month (cf. Rutherford & Westfall 1986). It seems likely that frosts in the grassland biome would cure the sward early in the dry season, and thus render them flammable throughout the dry season. For those woody species that are fire tolerant, such as savanna woody elements (McNaughton et al. 1982), the combination of cold temperatures and a prolonged fire season may contribute to their absence from the grassland biome as a whole. Savanna trees may be frost sensitive, and their distribution may be limited by the frequent occurrence of frost in the dry season. Occasional severe frosts in the savanna biome have resulted in widespread mortality of trees. Alternatively, it may be that cool temperatures at the beginning and end of the wet season in the grassland biome limit woody plant production sufficiently to preclude their establishment. In other respects the climate of the savanna biome is similar to the grassland biome, having a strongly seasonal summer rainfall that would permit the build-up of sufficient fuel to carry fire, and the presence of a marked dry season that causes the dessiccation of vegetation and therefore favours fire.

5.4.3 CLIMATE AND FIRE IN OTHER BIOMES

The humid conditions that prevail in forests reduce the occurrence of fire, except following a prolonged drought (Granger 1984, Clark 1988, 1989). This illustrates the effect of the (long-term) water balance in determining the occurrence of fire. In the arid and semi-arid areas of the succulent and nama-karoo biomes rainfall is sparse and erratic (Rutherford & Westfall 1986). This results in low primary productivity (Rutherford 1978, 1980) so that fuel loads accumulate slowly (Edwards 1984). Further, karoo plants tend to be spaced widely, reducing fire spread. Fires are therefore relatively rare in these biomes (Stuart-Hill & Mentis 1982, Edwards 1984, Rutherford & Westfall 1986), tending to occur following periods of unusually high rainfall. Fynbos vegetation is highly flammable due to the presence of combustible oils, finely divided canopies and relatively continuous structure (Rutherford & Westfall 1986). However, post-fire regeneration is relatively slow, requiring at least four to six years to accumulate sufficient fuel to sustain another fire (Kruger & Bigalke 1984). It seems that natural frequencies range from six to forty years (Kruger 1979), but generally would be more frequent than every 25 years (Rutherford

& Westfall 1986).

In summary it appears that climate contributes indirectly to the development of grasslands by maintaining a disturbance regime that excludes woody plants that are not fire tolerant. Species that are fire tolerant appear unable to tolerate low dry season temperatures in addition to a prolonged fire season. This hypothesis can only be tested with more intensive sampling of the interface between the grassland and the forest and savanna biomes. Further work also needs to attempt to develop models that predict fire frequency and intensity in different vegetation types, and under different climatic conditions.

5.4.4 WHAT ABOUT TOPOGRAPHY AND SOILS?

If fire is a major determinant of the distribution of the grassland biome, then it is necessary to have a topography that enables fires to spread over large areas i.e. gently undulating and unbroken. This feature was recognised for the North American grassland biome (Anderson 1982, Axelrod 1985). Fires have swept periodically over vast areas of the great plains of North America, and are considered to be correlated with the occurrence of the grassland biome there (Cooper 1961). Forests in Illinois, USA are confined to rugged topography associated with streams and glacial moraines, with grasslands occurring on level till plains (Rodgers & Anderson 1979). In most of the central plains of the USA grasslands occupy relatively level topography, with woodlands or forests restricted to rough dissected topography (Wells 1965, 1970). South Africa's grassland biome is situated on a gently undulating land surface (Mentis & Huntley 1982, Partridge & Maud 1987), which would have enabled fires to spread over vast areas. Most experience with grassland fires today is limited to prescribed burns, frequently under conditions that permit easy fire control. As a result there is relatively little information on fire under pre-colonial conditions which may have maximised fire spread or damage to woody plants (du Toit 1972, Trollope 1973, 1974).

A further important determinant of fire behaviour is the result of interactions during the fire season of topography and wind. Sites on steep leeward slopes are likely to be protected from fire, and therefore have woody plants in greater abundance than

windward slopes (van Daalen & Geldenhuys 1988, Geldenhuys Personal Communication[6]).

Past confusion regarding the roles of fire, climate, topography and soils in maintaining grasslands, appears to have been due to these factors not having separate, unrelated effects. Local topography influences the spatial arrangement of grass tufts, with the increased microrelief associated with rock outcrops decreasing plant density and therefore the potential fuel load. It also creates discontinuities that would reduce fire spread (Everson et al. 1988). Soils with poorly developed illuvial B-horizons, are correlated with sites of high microrelief or exposed bedrock, and therefore with low fire frequency or intensity. The suggestion that soils determine the distribution of the grassland biome as a whole (Feely 1987) is therefore considered spurious. At smaller spatial scales the distribution of woody plants in the grassland biome is associated with differences in soil types (Ellery et al. in press), but these may be the result of the effect of soil surface characteristics on the fire regime rather than of the soil on the vegetation *per se*.

5.5 SUMMARY: A SYNTHESIS OF THE ROLES OF CLIMATE AND FIRE

A synthesis of results from last two chapters is summarised in Figure 5.9. It shows the perceived role of climate, topography, soils, grazing and fire in giving rise to the grassland biome, and to wooded and non-wooded patches within the grassland biome. Rainfall is moderate to high, is strongly seasonal, and occurs in summer. The combination of intermediate to high rainfall, and warm temperatures during the wet season are climatic features that promote high wet season plant production, and therefore the establishment of a high standing crop. Low temperatures in the dry season, and the occurrence of frosts, may cure the sward early in the dry season. This renders the sward flammable for longer than in other biomes, where rainfall is intermediate to high, and where it is strongly seasonal and in summer (e.g. savanna biome). Warm, dry winds in winter in the moist grasslands east of the Great Escarpment desiccate the sward, once again enhancing its susceptibility to fire.

[6] C.J. Geldenhuys, FORESTEK, CSIR, PO Box 395, Pretoria, South Africa.

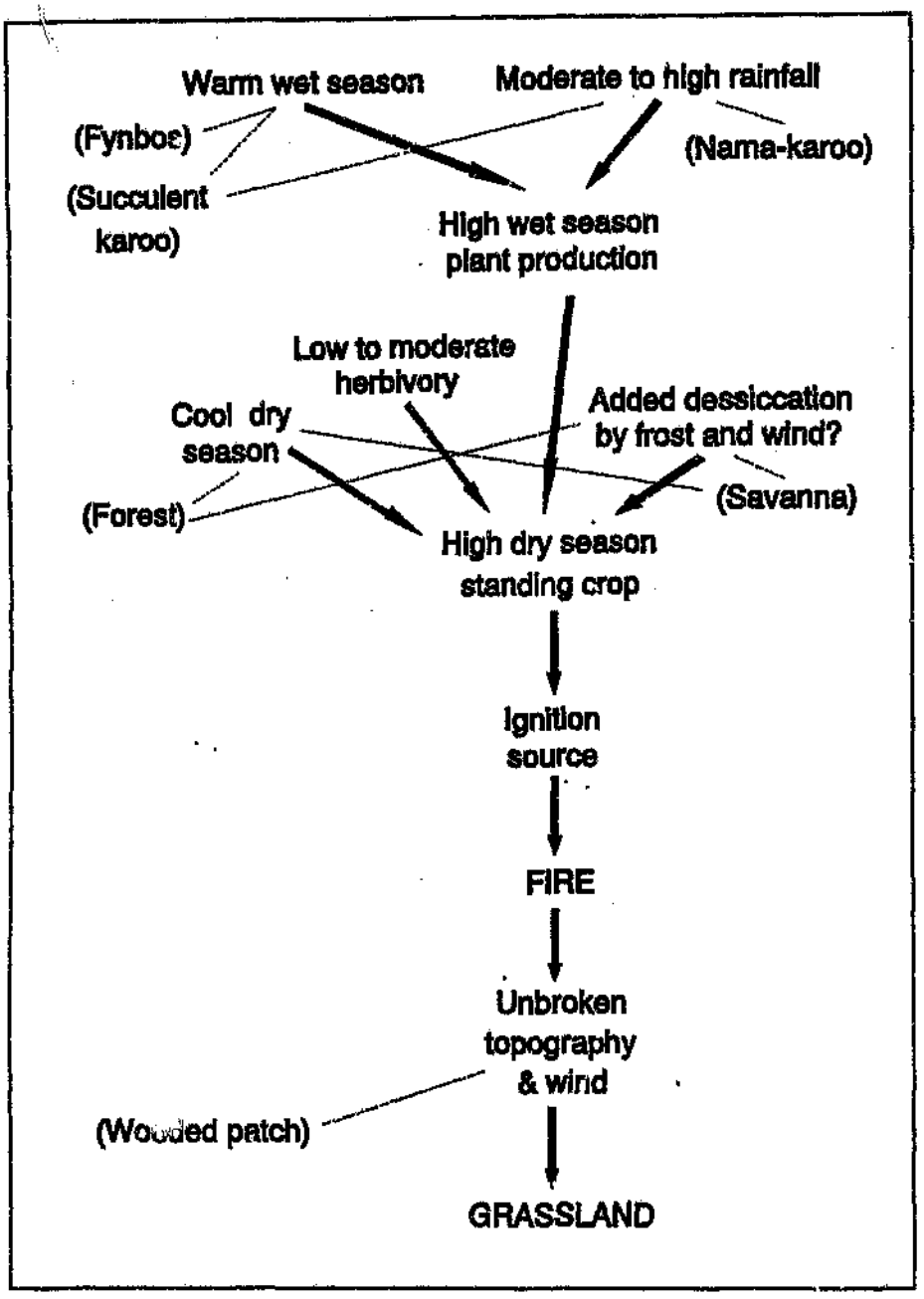


Figure 5.9: A diagram summarising a conceptual model of the distribution of grassland and wooded vegetation units. Solid arrows indicate the outcome of a process or event, but dashed lines indicate the outcome should the condition not be met in the scheme.

Lightning strike intensity is higher in the grassland biome than in other biomes. Being a natural ignition source, it would have caused fires prior to the time that humans used fire as a tool to concentrate game locally, and in the management of natural pastures for livestock. Provided that herbivores do not remove the bulk of the wet season standing crop, fires would occur frequently.

A further condition is necessary for the existence of a grassland biome. It requires a relatively unbroken topography so that fire can spread. The existence of wooded patches in the shadow areas of the prevailing winds during the dry season in the grassland biome supports this suggestion.

All of the conditions need to be met in the scheme presented in Figure 5.9 for the existence of the grassland biome. Its distribution is therefore under the overall control of climate, which promotes frequent burning for a prolonged period each year. Features of the environment that promote fire spread are also important in the maintenance of the grassland biome.

CHAPTER 6

IDENTIFYING THE MAJOR FUNCTIONAL FEATURES OF SOUTH AFRICA'S GRASSLANDS

6.1 INTRODUCTION

Within South Africa's grassland biome, a number of structural and functional types have been recognised. One aspect that has been dealt with thus far has been the distinction between 'true' and 'false' grasslands (Acocks 1975). This distinction has formed the basis of many rangeland management practices in South Africa, particularly in terms of developing objectives and policies for burning (Tainton 1981). The distinction of sweetveld, mixed veld and sourveld is another component of a range of possible adaptive responses of vegetation to the environment. A structural criterion used to distinguish different grassland types is based on the height of the sward (tall vs. short grassland types). Seldom have studies focused on more than one or a few of these characters at a time in an attempt to develop an objective structural or functional classification. The aim of this section of the study was to identify, using objective techniques, the response of a range of functional characteristics of grassland plants to the environment.

6.2 METHODS

6.2.1 VEGETATION SAMPLING AND SITE DESCRIPTION

Grassland vegetation was sampled in 101 study sites in 10 study areas within the grassland biome (Fig. 6.1a). Study areas were selected to cover a wide range of temperature and moisture conditions (Fig. 6.1b). Within each study area sites were chosen to cover a wide range of soil types, landscape positions and management regimes.

The grass layer at each site was sampled using the point-to-plant and plant-to-nearest-neighbour method of Cox (1976). The basal circumference of each tuft encountered

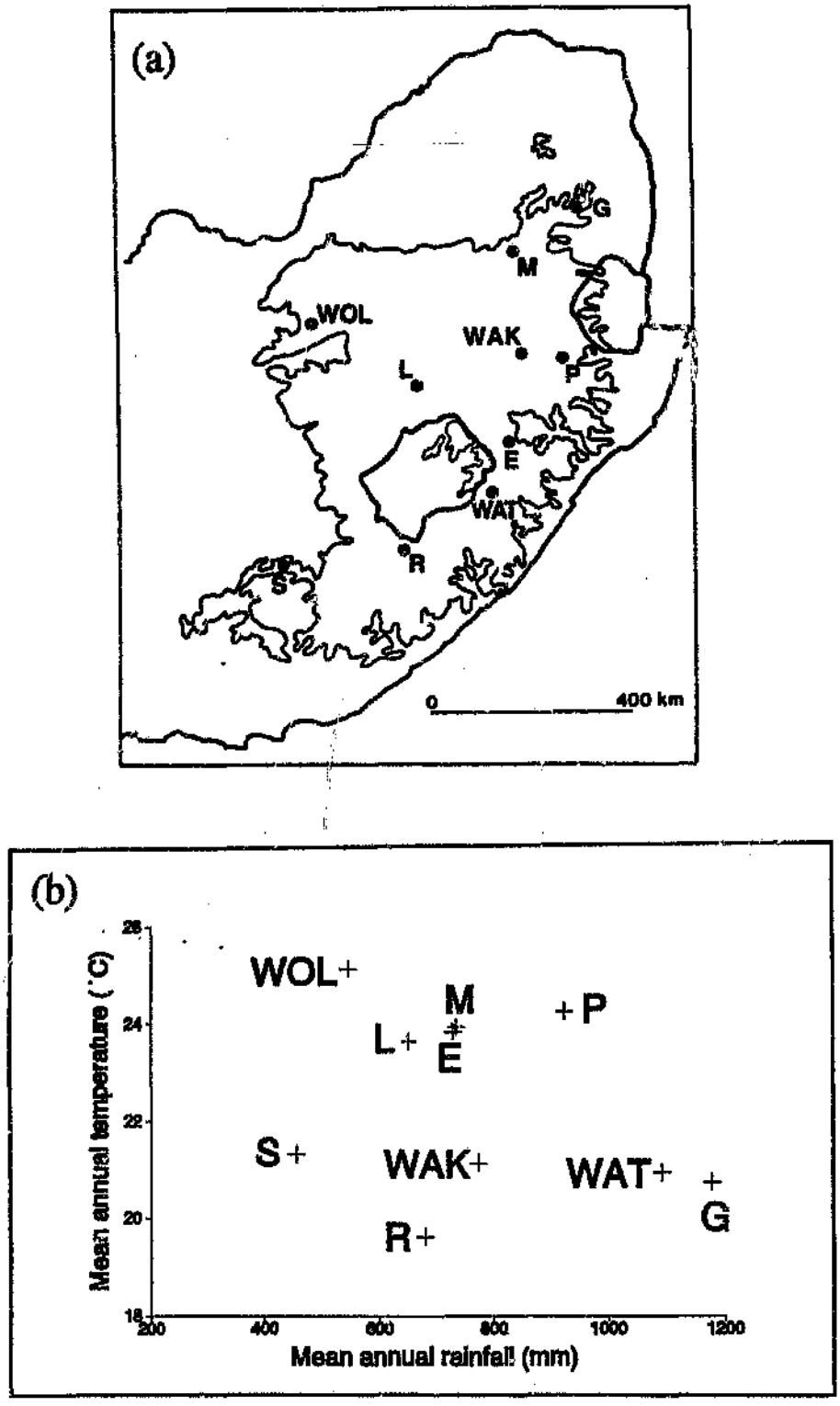


Figure 6.1: The distribution of study areas within the grassland biome (a) and the range of mean annual temperature and precipitation covered by the selection of these sites (b). Abbreviations for the place names and the number of stations at each site are as follows: E = Estcourt, 7; G = Graskop, 10; L = Lindley, 7; M = Middelburg, 9; P = Paulpietersburg, 8; R = Rhodes, 15; S = Steynsburg (Platoskamp), 10; WAK = Wakkerstroom, 11; WAT = Waterford, 13; WOL = Wolmaransstad, 11.

during sampling was measured. The data were used to calculate density and basal cover for each species at each site. Site characteristics measured were the same as those described in the previous chapter, namely slope, aspect, slope variability, fire frequency and grazing intensity. Soil profile descriptions and sampling were also done as described in the previous chapter.

6.2.2 CLIMATIC MODELLING

Local climate was modelled as described in the previous chapter (Figs. 5.2 & 5.3).

6.2.3 SOIL ANALYSES

Soil samples were taken from each horizon providing an average of three samples per profile. In addition to these, composite surface soil samples were taken to a depth of 0.1 m from 25 evenly spaced points in each plot. Soil texture, bulk density and organic carbon content were measured for samples from the soil pits using the techniques described in the previous chapter. Exchangeable calcium, magnesium and potassium contents were measured on the same samples using a 1M ammonium acetate extraction and measuring concentration by atomic absorption spectroscopy. Total nitrogen, an index of readily mineralizable nitrogen and extractable phosphorus were determined for each of the composite surface samples. Total nitrogen was measured by wet oxidation based on the Kjeldahl digestion using selenium as a catalyst (Keeney 1982). The digests were analyzed colorimetrically for nitrate by the salicylic acid method (Cataldo et al. 1975). The index of mineralizable nitrogen, a measure of the size of the readily mineralizable nitrogen pool, was measured by anaerobic incubation at constant temperature (40°C) for seven days (Keeney 1982). The supernatant solution was analyzed colorimetrically for ammonium using the technique of Dorich & Nelson (1983). Extractable phosphorus was measured by resin bag extraction (Amer et al. 1955, Sibbensen 1978) with concentration measured colorimetrically using the technique of Murphy & Riley (1962).

A number of indices of soil fertility were developed including the sum of calcium, magnesium and potassium for the A- and B-horizons (CMKA and CMKB respectively), and the standardised sums of calcium, magnesium, potassium, nitrogen

and phosphorus (NUT1), and of nitrogen and phosphorus (NUT2). Standardised values for each element were calculated using the minimum and maximum values of all samples. These were given values of 0 and 10 respectively. The remaining sample values were scaled arithmetically between these two extremes.

The environmental variables used in analysis of data from individual stands are summarised in Table 6.1.

6.2.4 DATA ANALYSES

6.2.4.1 INVESTIGATING RELATIONSHIPS BETWEEN SPECIES DISTRIBUTIONS AND ENVIRONMENTAL CONDITIONS

An indirect gradient analysis was performed using detrended correspondence analysis of the species by stands matrix as a primary matrix, with the environmental conditions by stands matrix as a supplementary matrix.

6.2.4.2 INVESTIGATING RELATIONSHIPS BETWEEN SPECIES DISTRIBUTIONS AND FUNCTIONAL CHARACTERISTICS

Characters considered of functional significance, such as photosynthetic pathway and growth form, were selected. Each species was assigned to an attribute class for each character. For example, attributes for the character 'growth form' were tufted, stoloniferous, rhizomatous or a combination of two or more of these attributes. The full list of functional characters selected, together with each of the attributes for each character, are given in APPENDIX 3. Species[1] were rated for each attribute based on the literature, examination of herbarium material, or observations made in the field. Species functional attributes for each character are provided in APPENDIX 4. A score for each functional attribute for each site was obtained by combining the species by functional data matrix (Fig. 6.2a), weighted by the basal area for each species, with the species by stands matrix (Fig. 6.2b) from data collected in the field, giving a stands by functional characters matrix (Fig. 6.2c).

---

[1] Species nomenclature follows Gibbs Russel et al. 1990.

Table 6.1: Environmental variables included in the species based ordination of stands as well as in the discriminant analysis of differences between sweetveld, mixed veld and sourveld sites in the study area, and abbreviations for each variable (see text, figures and tables that follow).

VARIABLE	ABBREVIATION
Duration of the growth season	GDAY
Growth season temperature	GTEM
No-growth season temperature	NGTEM
Sum of Ca, Mg & K in A-horizon	CMKA
Sum of Ca, Mg & K in B-horizon	CMKB
Extractable phosphorus (A-horizon)	PO4
Total nitrogen (A-horizon)	TOTN
Index of nitrogen mineralization	NMIN
Standardised sum of Ca, Mg, K, N & P in the A-horizon	NUT1
Standardised sum of N & P in the A-horizon	NUT2
Grazing history	GRHIS
Fire history	FIHIS
Slope	SLOPE
% sand (A-horizon)	SANDA
% clay (A-horizon)	CLAYA
% sand (B-horizon)	SANDB
% clay (B-horizon)	CLAYB

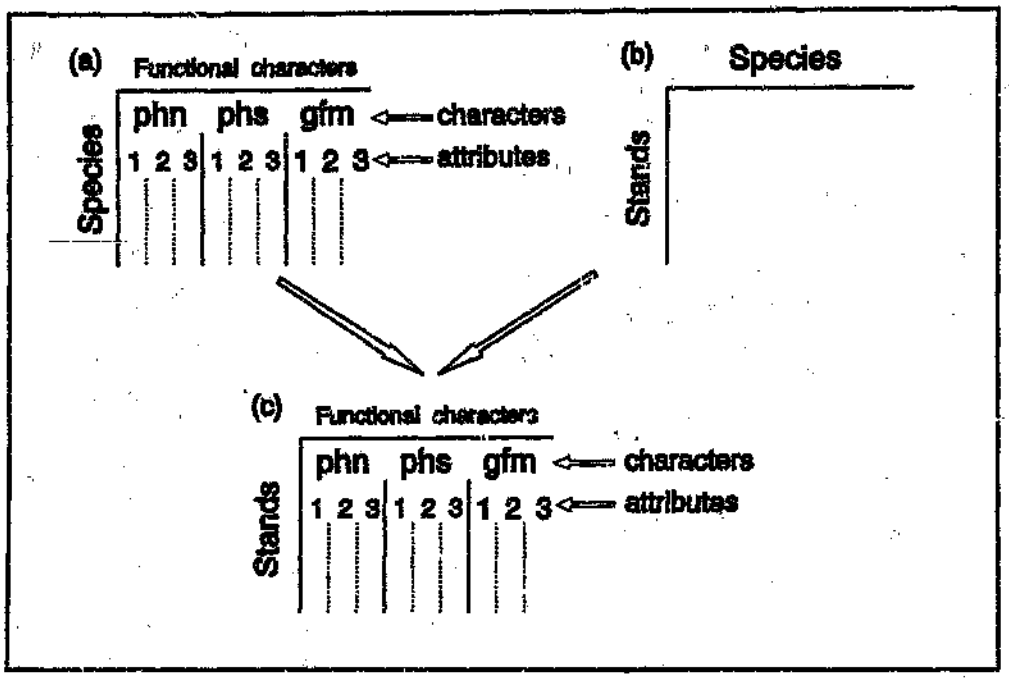


Figure 6.2: Schematic illustration of the way in which functional characters (with attributes and parameters) were scored for each species (a) and combined with the species by stands matrix (b) to produce a stands by functional characters matrix (see text for details).

This formed the basis of an exploratory investigation of relationships between the species ordination and the distribution of the functional attributes for each character. In order to ascertain how well the functional attributes for each character seperated from each other in ordination space, the functional attributes by stands matrices (one matrix for each character) were ordinated. Due to uncertainty regarding the nature of the functional attribute responses (linear vs. unimodal) for each character to the range of environmental conditions covered in the study, a principal components analysis (linear) and correspondence analysis (unimodal) were tried in each case. The success of each of the indirect gradient analyses is considered to be indicated by the sum of the canonical eigenvalues. In linear techniques such as principal components analysis, individual eigenvalues provide an indication of the percentage variance accounted for by each axis (ter Braak 1987). In weighted averaging techniques such as correspondence analysis, individual eigenvalues provide a measure of the separation of attributes for each character by each axis (ter Braak 1987). The sum of the canonical eigenvalues therefore provides some indication of how well the attributes for characters separate, and as such provides an indication of how well the ordination has performed. These values were used as a basis for selecting functional characters to be included in the ordination of species (and stands in the primary matrix) and functional characters (and stands in a supplementary matrix). In this way the geometry of the species based ordination formed the basis for the analysis of the distribution of functional characteristics.

6.3 RESULTS

6.3.1 ORDINATION OF THE SPECIES BY STANDS MATRIX USING DETRENDED CORRESPONDENCE ANALYSIS

The eigenvalues associated with the first four axes of the ordination of species and stands suggest that the first two axes were far more important than the second two in the separation of species and stands (Table 6.2). Fire frequency (FIHIS) and the duration of the growth season (GDAYS) were most highly correlated to the first axis of the ordination (Table 6.2), with both of these variables highly correlated to each other (Table 6.3). The first axis can be considered to represent a moisture gradient, with moist sites on the left and arid sites on the right (Fig. 6.3 a,b). The second axis

Table 6.2: Eigenvalues and weighted correlation coefficients of environmental variables with the first four species axes of the detrended correspondence analysis of species and sites.

VARIABLE	AXIS 1	AXIS 2	AXIS 3	AXIS 4
EIGENVALUE	.7372	.6840	.5085	.4483
GDAY	-.7448	.0310	-.1037	.0818
GTEM	.2118	.4956	-.2626	-.1072
NGTEM	.3335	.3492	-.2745	-.1954
CMKB	.4572	-.2568	-.0454	.0529
CMKA	-.0484	.0583	.1114	.0595
PO4	.3763	-.3839	-.2208	.0556
TOTN	-.4022	.0186	-.1416	.1923
NMIN	-.4367	-.0585	-.1869	.2079
NUT1	-.0586	-.2410	-.2556	.1845
NUT2	.2904	-.3267	-.1808	.1465
GRHIS	.4976	.0024	-.1323	.1363
FIHIS	-.7686	-.1005	-.0572	-.0445
SLOPE	-.0725	-.0750	.3655	.0056
SANDA	.0634	.1928	.3401	-.2371
CLAYA	.0387	-.1142	-.3559	.1268
SANDB	-.0218	.2390	.3951	-.2709
CLAYB	.2161	-.2440	-.4545	.2155

Table 6.3: Pearson's correlation coefficients of environmental variables included in the species based ordination. Correlation coeffiecients that are significant ($P<0.05$) are underlined.

VARIABLE	GDAY	GTEM	NGTEM	CMKB	CMKA	PO4	TOTN	NMIN
GTEM	-.212							
NGTEM	-.381	.933						
CMKB	-.592	-.184	-.029					
CMKA	.055	-.247	-.240	-.048				
PO4	-.356	-.151	-.030	.399	-.145			
TOTN	.500	-.239	-.359	-.085	.186	-.028		
NMIN	.445	-.271	-.348	.031	.045	.092	.757	
NUT1	.147	-.283	-.295	.200	.046	.640	.750	.645
NUT2	-.342	-.300	-.191	.825	-.018	.645	.370	.378
GRHIS	-.438	.064	.011	.384	.050	.193	-.115	-.158
FIHIS	.754	-.357	-.420	-.300	.037	-.251	.356	.402
SLOPE	.039	-.480	-.465	.072	.269	-.024	.205	.103
SANDA	-.046	.185	.179	-.376	-.007	-.214	-.331	-.541
CLAYA	-.127	.098	.131	.376	-.070	.130	-.009	.201
SANDB	-.045	.179	.177	-.350	-.022	-.168	-.290	-.481
CLAYB	-.183	.075	.126	.431	-.109	.189	-.071	.159

VARIABLE	NUT1	NUT2	GRHIS	FIHIS	SLOPE	SANDA	CLAYA	SANDB
NUT2	.712							
GRHIS	.041	.286						
FIHIS	.105	-.150	-.356					
SLOPE	.141	.144	-.131	.094				
SANDA	-.395	-.482	-.165	-.206	-.018			
CLAYA	.077	.303	.132	.064	-.138	-.811		
SANDB	-.334	-.433	-.194	-.132	.016	.900	-.714	
CLAYB	.071	.343	.125	-.079	-.208	-.717	.778	-.857

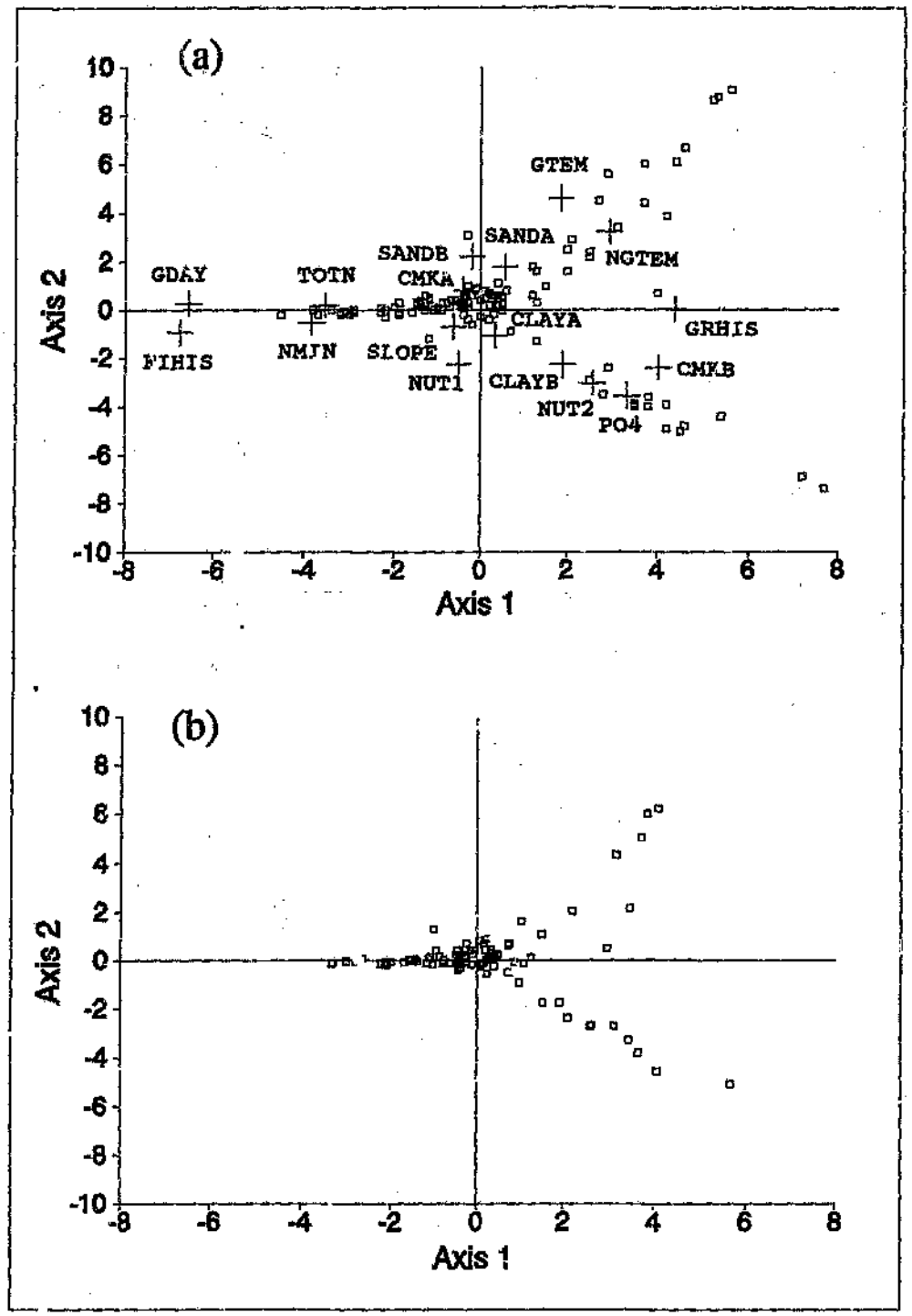


Figure 6.3: The ordination of species (a) and stands (b) on the first two axes of the detrended correspondence analysis (scores for species and stands on the first four axes are provided in APPENDIX 5). Superimposed on the species ordination are the centroids of each environmental variable (+). The mean values for the plots in each of the study areas for ordination axes 1 and 2 are provided in Figure 6.4a.

of the ordination was most highly correlated with the temperature during the growth season, with cooler conditions prevalent at the bottom and warmer conditions at the top of the second axis. The correlation between grassland composition and moisture and temperature is striking, as illustrated by comparison of the species and stand ordinations within a simple moisture-temperature plane (Fig. 6.4).

6.3.2 ORDINATION OF FUNCTIONAL CHARACTERS

The sum of the canonical eigenvalues of ordinations of functional characters is low for both principal components analysis as well as for correspondence analysis (Table 6.4). Of the 18 characters, 11 of the sums of eigenvalues were below 0.4 for principal components analysis, and 15 below 0.4 for correspondence analysis. For most of the characters (15), the sum of eigenvalues was greater for principal components analysis than for correspondence analysis (Table 6.4) suggesting a linear response for these characters over the range of environmental conditions sampled. This is expected since the value for each attribute of each character is the sum of a number of species attribute scores, and since the goal of a functional classification is to reduce the complexity that is characteristic of species based data. The remaining three characters indicate a unimodal response.

Attributes of the characters defence against herbivory and flowering phenology were most clearly separated over the range of samples, with reproduction and growth form also reasonably well separated (Table 6.4). The characters with the sums of eigenvalues greater than 0.4 in either the principal components analysis or the correspondence analysis were included in the analysis of the regression of functional characteristics with the species based ordination.

6.3.3 A SPECIES BASED FUNCTIONAL CLASSIFICATION OF GRASSLAND TYPES

The first axis of the output of functional attributes of characters, being correlated to the species based ordination, corresponds to increasing aridity, and the second axis to increasing temperature during the growth season (Fig. 6.3a). Characters have been grouped into those associated with growth form, reproduction, physiology and

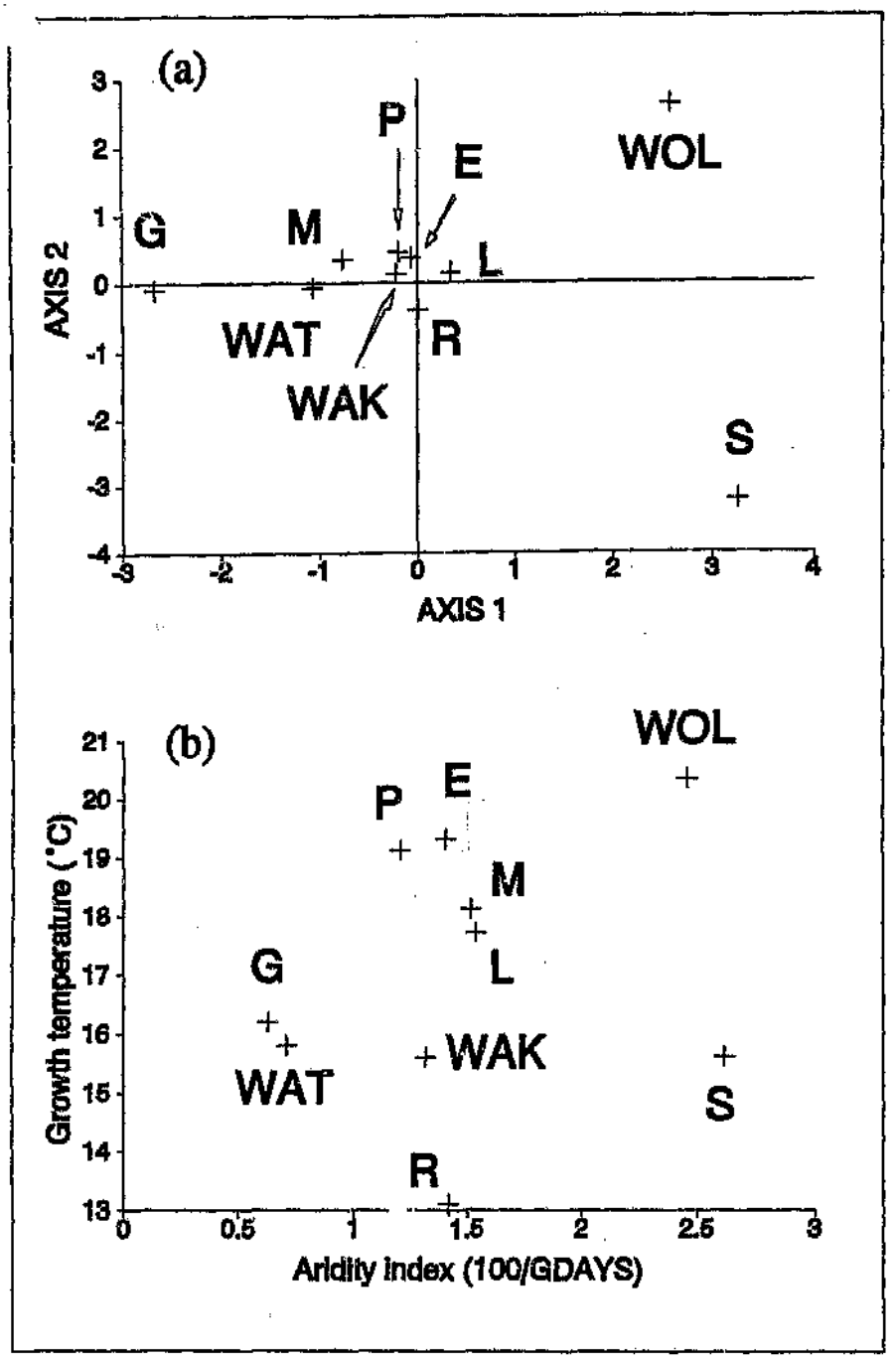


Figure 6.4: Comparison of the mean values of the species based ordination of stands (a; cf. Fig 6.3) with important features of climate (b). The climatic features are an aridity index and the growth season temperature. Abbreviations for study sites are: E = Estcourt, G = Graskop, L = Lindley, M = Middelburg, P = Paulpietersburg, R = Rhodes, S = Steynsburg (Platokamp), WAK = Wakkerstroom, WAT = Waterford, WOL = Wolmaransstad.

TABLE 6.4: The sums of canonical eigenvalues (TRACE) of the analyses of individual functional characters of grassland sites using principal components analysis (PCA) and correspondence analysis (CA).

FUNCTIONAL CHARACTERS	PCA TRACE	CA TRACE
PHENOLOGY	0.338	0.035
PHYSIOLOGY	0.304	0.406
REPRODUCTION	0.435	0.168
SEED SIZE	0.421	0.226
SEED NUMBER	0.420	0.253
DISPERSAL	0.288	0.160
LEAF PUBESCENCE	0.306	0.248
LEAF POSITION	0.278	0.147
HEIGHT	0.330	0.166
FLOWERING TIME	0.489	0.488
LEAF LENGTH	0.289	0.142
LEAF WIDTH	0.390	0.301
LEAF X/S SHAPE	0.373	0.299
DEFENCE	0.376	0.569
WOODINESS	0.401	0.284
GEOPHYTISM	0.411	0.425
PALATABILITY	0.404	0.394
GROWTH FORM	0.428	0.161

defence. Suggestions are made regarding the adaptive significance of the distribution of each of the attributes of each character in relation to the first two axes of the species based ordination.

6.3.3.1 GROWTH FORM CHARACTERISTICS

Functional characteristics considered to be related to growth form are growth form itself, the degree of geophytism and the woodiness of basal parts of the grass plant. The distribution of tufted forms, and tufted forms with rhizomes separates well along the first species axis (Fig. 6.5a), with tufted forms associated with high water availability, and tufted forms with rhizomes associated with low water availability. Other growth forms were very infrequently encountered, and omitted from the analysis. The increased dependence of offspring on the parent plant in tufted forms with rhizomes may be advantageous in arid situations where water stress is common, and where moisture and/or nutrient availability is possibly very patchy at a small scale due to the frequent occurrence of shallow soils.

There appears to be an increase in the occurrence of species with greater degrees of geophytism with increased moisture availability (Fig. 6.5b). In grasses geophytism appears to be more an adaptation to increased fire frequency than aridity. The distribution of plants with woody basal parts increases with increasing aridity (Fig. 6.5c), with the exception that plants with no evidence of increased woodiness are also common in arid areas. These are the annual grasses that are more common in arid situations. An increase in the degree of woodiness of basal parts appears to increase the storage of carbohydrate as well as possibly of water, which would assist in rapid and prolonged growth after a rainfall event.

6.3.3.2 REPRODUCTION

The predominant mode of reproduction, seed size, seed number and flowering phenology are the characters of longevity and reproduction that have been best indicated over the range of environmental conditions sampled in the study.

There is a decrease in the degree of sexual reproduction with decreased moisture

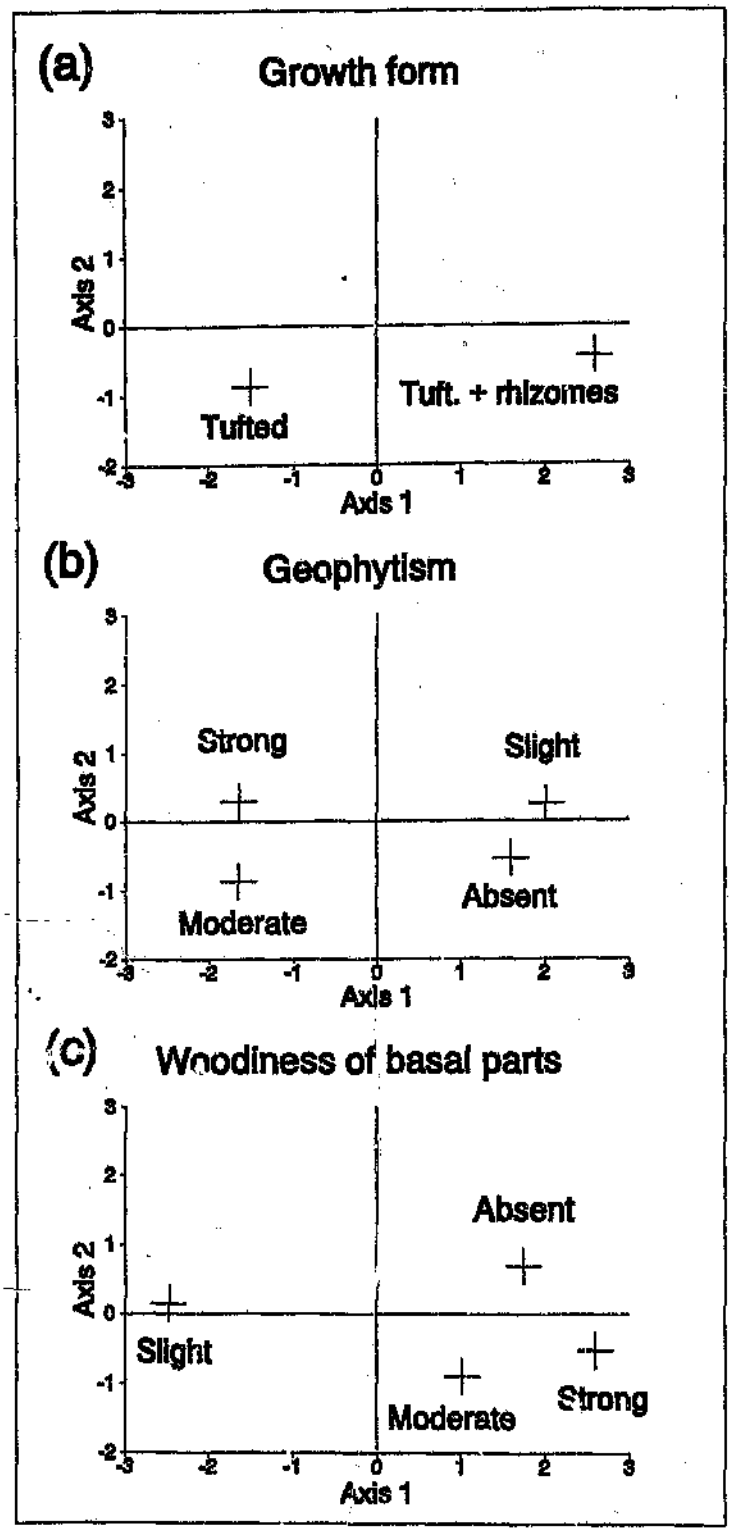


Figure 6.5: Ordination of growth form characteristics as supplementary matrices to the species and stands ordination, showing growth form (a), geophytism (b) and woodiness of basal parts (c).

availability (Fig. 6.6a). This reflects the greater contribution of tufted plants with rhizomes in arid areas, which have the potential to reproduce asexually. Tufted forms predominate in moist areas, and these were assumed to be obligate sexual reproducers, although under heavy grazing they may in fact break up to form a number of individuals.

Seed size decreases with increasing aridity (Fig. 6.6b), but the number of seeds produced increases with increased aridity (Fig. 6.6c). The production of large numbers of small propagules by annuals is clearly reflected in these relationships, but it is also the case that many of the perennial grasses in arid areas (such as many species of Aristida) produce a large number of small seeds. This is suggested to be the result of decreased competition, and increased environmental control of a plants success in arid environments. Seeds of grasses are short lived, and in the spatially and temporally heterogeneous environment of arid habitats, the production of a large number of small seeds appears to be favoured. In the more predictable environment of moist habitats, the production of a few large propagules appears to offer increased competitive ability during early seedling development.

Flowering phenology in wet areas occurs throughout the growth season, or else early in the growth season, with progressively later flowering as aridity increases (Fig. 6.6d).

6.3.3.3 PHYSIOLOGY

The distribution of grasses with different photosynthetic pathways is related to both axes of the species based ordination (Fig. 6.7). Grasses that are intermediate between the C3 and C4 pathways, and therefore exhibit either of these two pathways are most frequent in moist situations. Those with the NAD-me pathway occur primarily in arid situations. The C3 pathway is predominant in cool, relatively moist situations, and the PCK pathway in warm areas of intermediate moisture availability. The NADP-me pathway is relatively close to the origin, apparently tending to predominate in more mesic situations. These may reflect the outcome of competitive interactions in a given moisture/temperature regime, where the optimum moisture and temperature conditions for plants with each of these photosynthetic pathways differs. For

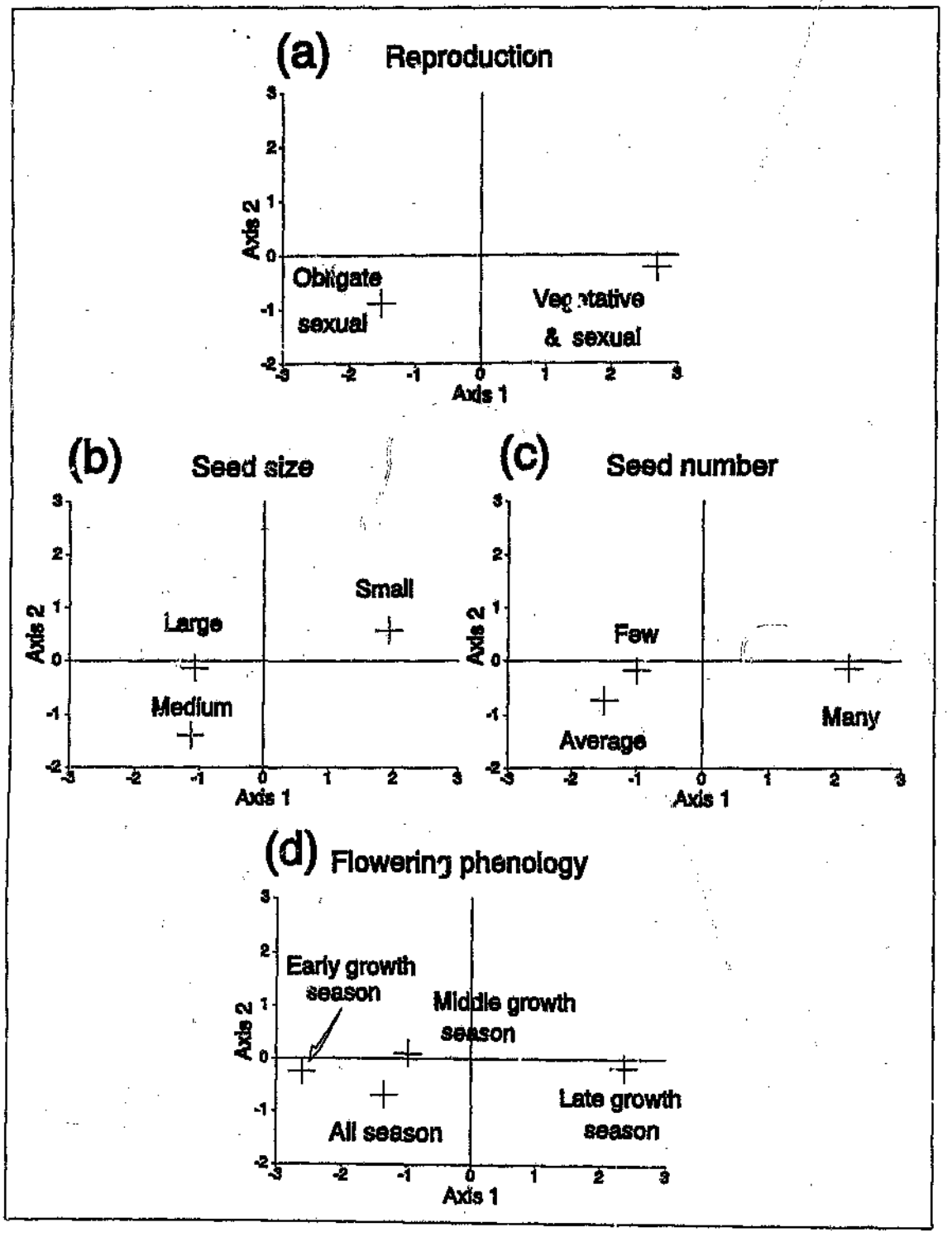


Figure 6.6: Ordination of characters associated with reproduction as supplementary matrices to the species and stands ordination, showing the predominant mode of reproduction (a), seed size (b), seed number (c) and flowering phenology (d).

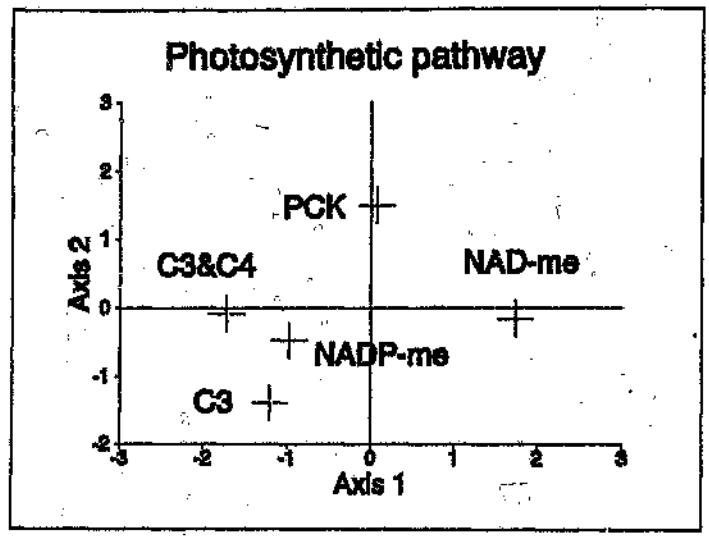


Figure 6.7: Ordination of physiology as a supplementary matrix to the species and stands ordination.

example, the optimum temperature for C_4 plants is higher than for C_3 plants, and C_4 plants (Pearcy & Ehleringer 1984) may therefore be expected to outcompete C_3 plants in warmer situations. Similarly, the water use efficiency of C_4 plants is greater than for C_3 plants, and species with the C_4 photosynthetic pathway may therefore be expected to outcompete those with the C_3 photosynthetic pathway in more arid situations.

6.3.3.4 DEFENCE AND PALATABILITY

The nature of plant defence against herbivory is correlated to moisture availability, with grasses that have been recorded as producing tannin-like substances being most abundant in moist sites, and those with other forms of defence (wiregrasses, growth form, or with no obvious defence) in more arid situations (Fig. 6.8a). Grasses defended with terpenes, or the 'mtshiki' grasses (those with leaves that are particularly strong and difficult to break, so that when they are grazed, the whole plant tends to be pulled out of the ground) occur in areas of intermediate water availability. A gradient from sourveld to mixed veld to sweetveld is evident with increasing aridity (Fig. 6.8b). Sourness appears to be correlated with the duration of the growth season, as well as with the occurrence of tannin-like substances in grasses.

6.3.3.5 A PRELIMINARY FUNCTIONAL CLASSIFICATION: PROFILES OF SPECIES THAT OCCUR IN MOIST, INTERMEDIATE AND ARID AREAS

The distribution of attributes in relation to the first axis of the species based ordination provides a useful basis for developing a preliminary functional classification. The first axis can be divided into approximately three equal sections, representing a gradient from moist to intermediate to arid (Table 6.5). Although the arrangement of attributes in relation to the second axis reflects their occurrence in relation to the growth season temperature, no clear groupings are evident, and it will thus not be included explicitly as a factor in the present analysis.

Tufted perennial grasses that are moderately to strongly geophytic, and which do not have strongly woody basal parts tend to predominate in moist areas. Leaves tend to

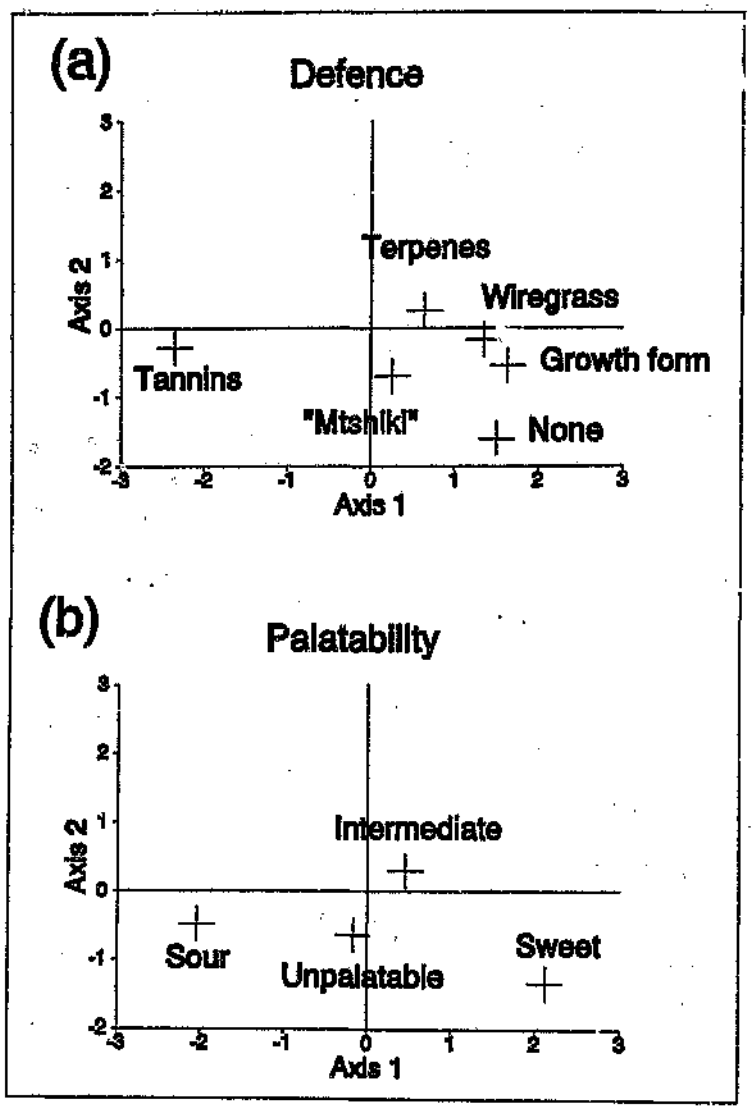


Figure 6.8: Ordination of characters associated with defence (a) and palatability (b) as supplementary matrices to the species and stands ordination.

Table 6.5: The distribution of attributes of functional characters in relation to moisture availability, giving some impression of the functional profiles of grasslands that might be expected along the moisture gradient.

FUNCTIONAL CHARACTER	MOIST	INTERMEDIATE	ARID
GROWTH FORM	Tufted		Tufted with rhizomes
GEOPHYTISM	Strong Moderate		Slight Absent
WOODINESS OF BASE	Slight		Strong Moderate Absent
REPRODUCTION	Sexual		Vegetative or sexual
SEED SIZE	Large Medium		Small
SEED NUMBER	Average Few		Many
FLOWERING PHENOLOGY	Early Middle Throughout		Late
PHOTOSYNTHETIC PATHWAY	C_3 & C_4 C_3 NADP-me	PCK	NAD-me
DEFENSE	Tannins	Unpalatable 'Mtshiki' Terpenes	Wiregrass Absent Growth form
PALATABILITY	Sour	Intermediate Unpalatable	Sweet

e defended with tannin-like substances, and the sward tends to be sour. Flowering is relatively early, or else occurs throughout the growth season, with obligate sexual reproduction a common feature. A small to intermediate number of seeds is produced, and the seeds are generally larger than in more arid situat ıs. The predominant modes of photosynthesis are C3, intermediate forms with both C3 and C4 pathways or NADP-me. The C3 pathway is predominant at relatively high moisture availability and at low temperatures.

At intermediate moisture availabilities, many of the attributes are intermediate between those of moist and arid sites. Attributes that appear more frequent in sites of intermediate moisture availability include defence with terpenes or the 'mtshiki' grasses. Although grasses of intermediate palatability predominate, species that are unpalatable are also common. The PCK photosynthetic pathway tends to be most common in areas of intermediate moisture availability.

Perennial grasses in arid areas tend to be tufted with rhizomes. Basal parts tend to be more woody than in moist areas, with the exception of annual species which do not show any signs of woodiness, and geophytism is generally slight or absent. Wire grasses tend to be more abundant in arid areas as do those that defend themselves by prostrate growth forms, or having stolons that are buried. Sweet grasses are more widespread in arid areas. Flowering appears to be late in the growth season, although species that reproduce vegetatively as well as sexually are more common than in moist areas. It appears that a relatively large number of small propagules are produced by species in arid areas, and species with the NAD-me photosynthetic pathway are common.

6.3.4 FOCUSING IN ON SWEETVELD, MIXED VELD AND SOURVELD

One of the best known but least understood characteristics of South Africa's grasslands is the occurrence of sweetveld, mixed veld and sourveld. The gradient from sweetveld to sourveld along the first axis of the species based ordination is clearly illustrated, as is the correlation of the distribution of these grassland types with different types of defence (Fig. 6.8 a,b). The ordination further suggests that the distribution of these veld types is related to water availability.

The species-based classification of stands illustrates the relationship between the first axis and the distribution of sweetveld, mixed veld and sourveld even more clearly. The distribution of sites sampled in this study in each of these three veld types (after Acocks 1975, Tainton 1981) have been superimposed on the species based ordination (Fig. 6.9). Sourveld occurs in areas with a high number of growth days, mixed veld in areas where the growth season is of intermediate duration, and sweetveld in areas where the growth season is short.

6.4 DISCUSSION: COMPARISON OF THIS APPROACH WITH OTHER APPROACHES

The classification of the veld types of South Africa (Acocks 1975) was explicitly based on floristic criteria. The final classification however, emphasised differences in floristic, structural, functional and habitat characteristics. The basis for distinctions made between the veld types in South Africa are however not clearly described, and for that reason appear somewhat arbitrary.

While the present study has not produced a new classification of vegetation types, of the nature provided by Acocks (1975), it illustrates the nature of grassland functional response to an important environmental gradient, moisture availability. Features of grassland plants that vary in apparent response to this gradient are varied, and include aspects of plant growth form, degree of geophytism, woodiness of basal parts, aspects of reproduction, photosynthetic pathway, defence and palatability. Each of the attributes of these characters are important in their own right, apparently varying in response to moisture availability or a correlate of moisture availability, such as fire frequency or fire intensity. Some of the characters are important from a biological point of view, such as the distribution of species with different photosynthetic pathways. There may be aspects of the distributions of these plants that are important from a functional perspective, such as grassland productivity under given climatic and edaphic conditions (Pearcy & Ehleringer 1984). An understanding of the determinants of grassland types that have combinations of taxa with different photosynthetic pathways may be important in predicting the outcome for grassland productivity of different scenarios of environmental change, especially climate change. Other characters may be important from an applied perspective. If one we

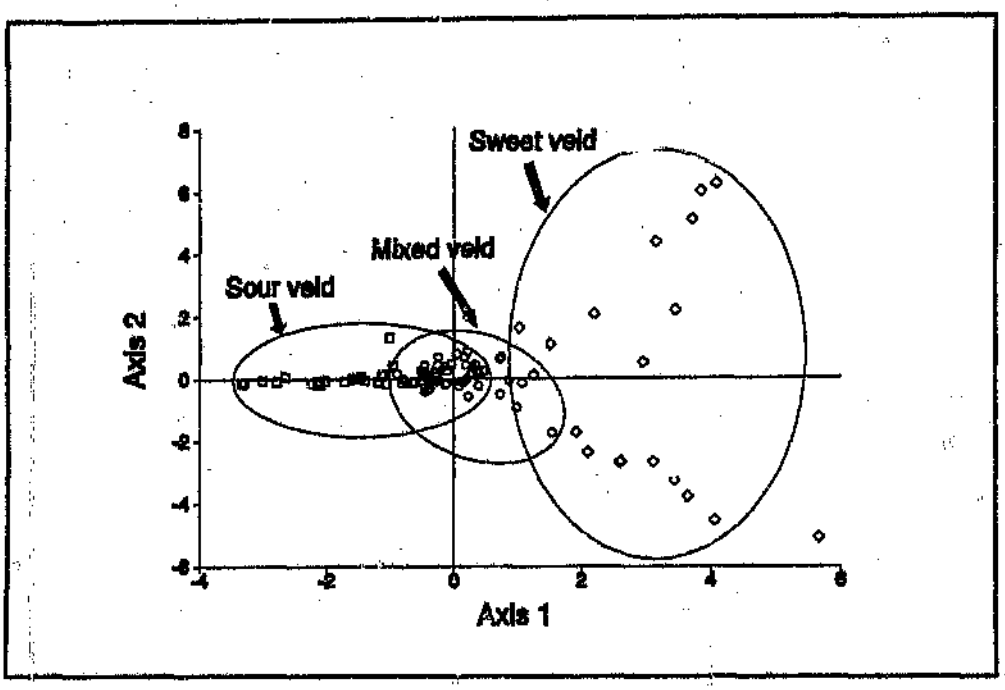


Figure 6.9: The distribution of sites sampled in vegetation types classified by Acocks (1975) as sourveld (□), mixed veld (○) and sweetveld (◇) in relation to the first two axes of the species based ordination of stands. The first axis represents a gradient of moisture availability, with moist sites on the left, and arid sites on the right. The second axis corresponds to an increase in the wet season temperature.

focusing on compositional change that may result from different combinations of grazing and drought one might choose to focus on a combination of characters related to reproductive characters and defence (O'Connor 1991).

The widely recognised distinction between sweetveld, mixed veld and sourveld has been highlighted in this study. The distribution of these veld types in relation to a moisture gradient is illustrated, both in the distribution of functional characteristics in the functional ordinations, and also in the distribution of stands in these veld types in the species based ordination. Their distribution appears to be correlated with water availability, a feature recognised in the literature (Tainton 1981, Zacharias 1990). This functional characteristic has been chosen due to its importance from a rangeland management perspective in South Africa, and forms the subject of the following chapter.

6.5 SUMMARY

The relationship between the distribution of species, and the occurrence of functional characters has been investigated. In particular, plant growth form, the degree of geophytism, the woodiness of basal parts, aspects of reproduction (mode of reproduction, seed size, seed number and flowering phenology), photosynthetic pathway, plant defence and palatability have been highlighted. These features have been synthesised in a preliminary functional classification that emphasises the functional profiles of grasslands that might be expected along a moisture gradient within the grassland biome.

The distribution of sweetveld, mixed veld and sourveld along this moisture gradient is of particular interest, as it is one of the most widely recognised functional features of the grasslands of South Africa, and forms the basis for many rangeland management practices in the country.

CHAPTER 7

TOWARDS PREDICTIVE UNDERSTANDING OF THE DETERMINANTS OF SWEETVELD AND SOURVELD

7.1 INTRODUCTION

7.1.1 THE DISTINCTION OF SWEETVELD AND SOURVELD

The most fundamental distinction in grassland management in South Africa is between sweetveld, mixed veld and sourveld. In essence, livestock feeding on sourveld tends to lose body weight during the dry season due to a decline in forage quality below the level for efficient digestion (Fig. 7.1). In sweetveld however, forage quality never declines such that animals cannot maintain growth. Mixed veld is intermediate between these two extremes. Despite the importance of the distinction between sweetveld and sourveld, the distribution of these vegetation types, their seasonal forage quality dynamics, and their responses to certain manipulations are poorly understood (cf. Tainton 1981, Kirkman 1988, Zacharias 1990). The objective of this section of the study was to develop predictive understanding of the distribution of sweetveld, mixed veld and sourveld.

The terms 'sweetveld' and 'sourveld' were in use prior to the commencement of formal rangeland science in South Africa (Alberti 1807). Their altitudinal and geographic separation was discussed by Pole Evans in 1920. More formal definitions were only published much later (Scott 1947), with current definitions being subjective and essentially descriptive. Definitions provided below are a summary of Tainton (1981) and Zacharias (1990).

- Sourveld provides palatable material only during the growing season, and is unpalatable when mature. It provides grazing for 6 months or less.
- Sweetveld is palatable even when mature, and therefore provides grazing throughout the year.
- Mixed veld is intermediate between sourveld and sweetveld, providing grazing for between 6 and 11 months of the year.

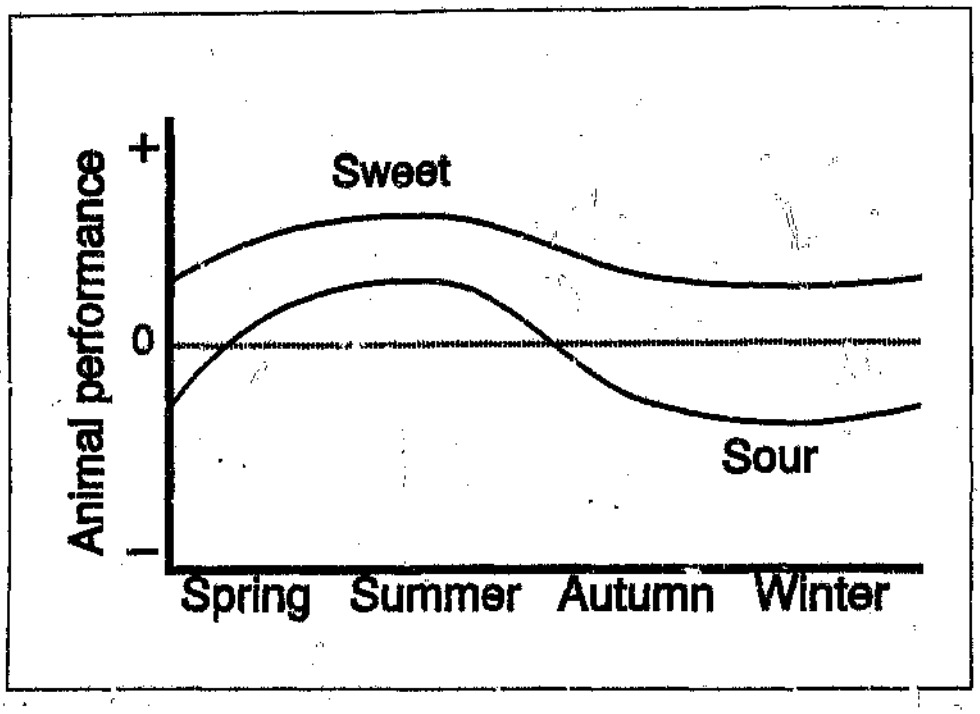


Figure 7.1: Schematic illustration of animal performance in sweetveld and scurveld at different times of the year assuming low stocking rates. Differences in animal performance are due to forage quality rather than avalaility.

Because of the decline in forage quality in sourveld late in the wet season and into the dry season, graziers have historically used a system of 'trek' farming. Sourveld areas are used during the summer months when this veld is productive and palatable. Stock is moved to sweetveld areas late in the wet season to overwinter. It seems likely that Iron Age farmers used a similar system of moving cattle between sourveld and sweetveld areas in southern Africa (Alberti 1807), and that Stone Age people followed indigenous game species as they migrated seasonally between sweetveld and sourveld areas (Carter 1970).

Sourveld areas tend to accumulate standing dead grass since it is unacceptable to grazers, and it needs to be burned occasionally in order to keep productivity and palatability high (Tainton 1981, Edwards 1984, Tainton & Mentis 1984). Fire has long been recognised as a tool to improve forage quality in sourveld areas, as illustrated by the burning practices of Stone Age hunter gatherers who burned veld to concentrate game locally (Carter 1970, Maggs 1984). Even with burning, forage quality varies seasonally in sourveld. Grazers in sweetveld areas however, tend to consume dead grass leaf material, so that if the stocking rate is sufficiently high, it may not be necessary or even possible to burn (Edwards 1984).

The distribution of sweetveld, mixed veld and sourveld has been summarised by Tainton (1981). Sweetveld occurs in hot, dry situations at relatively low elevation and sourveld occurs in cool, moist situations at high elevation. Two detailed studies aimed at elucidating the determinants of the distribution of sweetveld and sourveld, both confined to the grasslands east of the great escarpment, found sourness to be correlated to elevation (Kirkman 1988, Zacharias 1990). This was suggested to be a spurious association - particularly if grasslands elsewhere in the country were considered (Zacharias 1990). The general trend in the occurrence of sweetveld and sourveld is obscured by the large number of exceptions if their occurrence is plotted against any one of these factors independently.

The approach in this component of the study has been to develop an hypothesis of the distribution of sweetveld and sourveld based on the literature. The hypothesis was tested at two scales of resolution. The role of climate and parent material was investigated at a broad (subcontinental) scale using data for weather stations in known

veld types and on known parent material. This broad-scale study was complimented by another study at a more detailed scale of resolution in which the role of soil fertility was quantified.

7.1.2 AN HYPOTHESIS OF SWEETVELD AND SOURVELD DISTRIBUTION

7.1.2.1 THE RESOURCE AVAILABILITY HYPOTHESIS

Diet selection by grazing herbivores has traditionally emphasised optimization of nutrient or energy intake (Westoby 1974, Sinclair 1975). This theoretical framework was developed in grassland ecosystems, in which the production of secondary chemicals as herbivore deterrents was considered unimportant (Bryant et al. 1992). More recently, antiherbivore defence has been recognised as an important determinant of diet selection by browsing herbivores (Bryant & Kuropat 1980, Owen-Smith & Novellie 1982). Different woody plant species produce different types and quantities of secondary chemicals that deter herbivores, and thereby influence forage selection.

Based on patterns of response by plants typical of habitats with different resource availabilities (particularly soil nutrients and light), the evolutionary response of plants to herbivory has been related to their total environment. The balance of carbon assimilation and nutrient acquisition is considered to be particularly important in determining the nature of a plant's defence against herbivory (Bryant et al. 1983, Coley et al. 1985, Chapin et al. 1986, Bazzaz et al. 1987). Plants typical of resource limited environments, such as those with infertile soils, generally have low growth rates, as they cannot acquire sufficient resources for rapid growth (Grime 1977, Chapin 1980). Loss of plant parts to herbivory represents a greater loss of the capital resources and net production in these slow-growing species, than in fast growing species typical of resource-rich environments. As a result there is a general correlation between plant antiherbivore defence and resource limitation (Bryant et al. 1983, Coley et al. 1985). Species characteristic of resource-rich environments have been selected for rapid growth so as to outcompete their neighbours and dominate available resources (Chapin 1980).

Whether the resource availability hypothesis applies to grazers feeding on grasses or

not has not yet been established. In the light of the recent discovery of the widespread occurrence of condensed tannins and tannin-like substances in southern African grasses (Ellis 1990, du Toit et al. 1991), the resource availability hypothesis may be useful in interpreting interactions between grazing animals and graminoids, and particularly in explaining the distribution and seasonal forage quality dynamics of sweetveld and sourveld. The occurrence of tannin-like substances in grasses in the grassland biome was shown in the previous chapter to be correlated to the occurrence of sourveld, suggesting that secondary metabolites may indeed be responsible for the observed forage quality dynamics in sourveld grasses.

The hypothesis of sweetveld and sourveld can be stated as follows. The distinction between sweetveld and sourveld is based on the seasonal pattern of forage quality, which is determined by its nutrient content, particularly nitrogen. The nutrient content is a function of the strength of nutrient supplying processes in the soil-plant system, relative to the strength of carbon assimilation metabolism of the plant. Where the environment favours nutrient assimilation relative to carbon assimilation, grasses will be sweet, and where the reverse is true, grasses will be sour.

The following sections contrast nutrient supplying processes, particularly with respect to nitrogen, with those involved in carbon assimilation. The underlying assumption is that forage quality is correlated to its protein quantity (Sinclair 1974, Mattson 1980), and thus reflects the carbon to nitrogen balance of the plant. Forage quality is also recognised to have several correlates, including fibre content and the *in vitro* dry matter digestability (Bransby 1981, Zacharias 1990). Although the hypothesis is based on nitrogen as a key nutrient, it can be applied to other organically bound nutrients such as phosphorus. The basic cations are not considered an important part of the hypothesis, because the hypothesis applies to organically bound nutrients, but they could be included using similar arguments.

7.1.2.2 DETERMINANTS OF CARBON ASSIMILATION

The rate of carbon assimilation in grasses is controlled by the activity of assimilatory enzymes in the leaf, leaf area, and by four environmental factors:

- **water availability** which controls stomatal conductance and hence the

diffusion of carbon dioxide into the leaf;

- **leaf temperature** which determines the balance between photosynthesis and respiration, and which regulates the activity of assimilatory enzymes;
- **radiant flux density** which controls the energy supply necessary for carbon assimilation; and the
- **carbon dioxide concentration of the atmosphere.**

Radiant flux density over both sourveld and sweetveld is equal and close to the saturation level for photosynthesis (Schulze & McGee 1978), and will be treated as a constant. Similarly, carbon dioxide concentration of the atmosphere is considered to be constant over the range of conditions covered by sourveld and sweetveld. Predictions regarding the effects of shading and global carbon dioxide increase can be made revisiting these assumptions once the model framework is in place.

The effect of increasing soil moisture content on carbon assimilation is illustrated in Figure 7.2a. At water contents below wilting point, plants are unable to assimilate carbon due to low stomatal conductances (Schulze 1986). As soil moisture increases, stomatal conductance increases and carbon assimilation increases in direct proportion to this (Wong et al. 1979). At soil water contents where water is freely available to plants, the activity of the carboxylation enzyme limits net carbon assimilation. In saturated soils there is a depression of net carbon assimilation due to the respiratory cost of having roots in anaerobic conditions (Armstrong 1975).

The response curve for carbon assimilation to leaf temperature has an asymmetric bell shape (Fig. 7.2b). The left hand portion follows the Arhennius law of exponentially increasing rate with increasing temperature, reflecting the response of enzyme activity to temperature. At high temperatures the respiration component overwhelms the photosynthesis component, causing net assimilation to decline abruptly. The temperature optimum for C_4 grasses is in the region of 27 - 30°C, while for C_3 grasses it is a few degrees lower (Pearcy & Ehleringer 1984).

7.1.2.3 DETERMINANTS OF NITROGEN ASSIMILATION

The nitrogen supply to grasses in natural grasslands is limited by the rate of

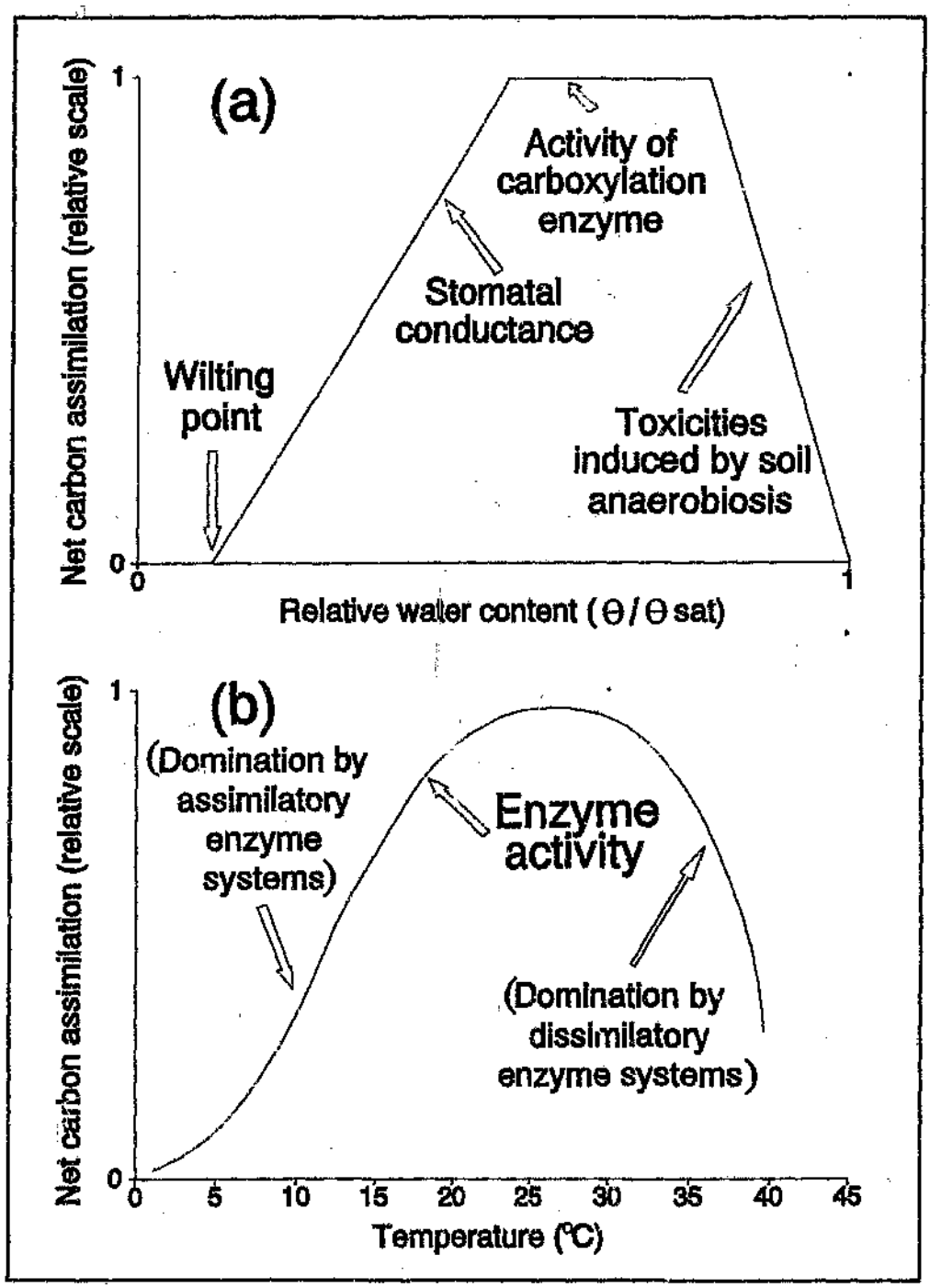


Figure 7.2: Net carbon assimilation in relation to soil moisture availability (a) and temperature (b). Annotations describe rate limiting processes.

mineralization of organic nitrogen in the soil, and not by the rate of plant uptake mechanisms for inorganic nitrogen (Chapin 1980). This is why significant amounts of inorganic nitrogen are seldom measurable in undisturbed soils. The rate of nitrogen mineralization in the soil is mainly controlled by three environmental factors:

- **the size of the readily mineralizable nitrogen pool in the soil;**
- **soil temperature;** and
- **soil water content** (Stanford & Smith 1972, Smith et al. 1977).

The size of the readily mineralizable nitrogen pool is related to the amount and nature of organic matter in the soil (Stanford & Smith 1972). The amount of organic matter which a soil can accumulate depends on the balance between production and decay, which is determined mainly by water availability, temperature, clay content and mineralogy, and the chemical composition of the litter. The chemical composition of litter relates largely to the quantity of leachable substances, nitrogen availability (C:N ratio of the litter), and the presence of lignin and polyphenols (Singh & Gupta 1977, Meetenmeyer 1978, Ellis 1990). Ultimately the amount of organic matter which a soil can accumulate is set by the degree to which organic matter is chemically or physically protected in the soil. This is a function of soil properties, including clay content and mineralogy (Griffin 1972, Dickinson 1974, Singh & Gupta 1977). Soil organic matter is stabilised by clays, particularly those with a large surface area such as the smectite group. In contrast, sandy soils and those originating from acid igneous rocks such as granites, tend to have low organic matter contents, and therefore low total nitrogen.

Water availability strongly influences the rate of nitrogen mineralization. As soil water increases, nitrogen mineralization increases (Fig. 7.3a), reflecting the activity of microorganisms in the soil. Soil microbes responsible for nitrogen mineralization are active in the soil at water potentials lower than plant wilting point (Sabey & Johnson 1971, Stanford & Epstein 1974). At high soil water contents, nitrogen mineralization is reduced due to the loss of mineralized nitrogen by denitrification (Stanford & Epstein 1974), reduced oxygen transport in the soil, and leaching.

The nitrogen mineralization response curve for low temperatures is an Arrhenius type relationship (Fig. 7.3b; Stanford et al. 1973, MacDuff & White 1985), with an

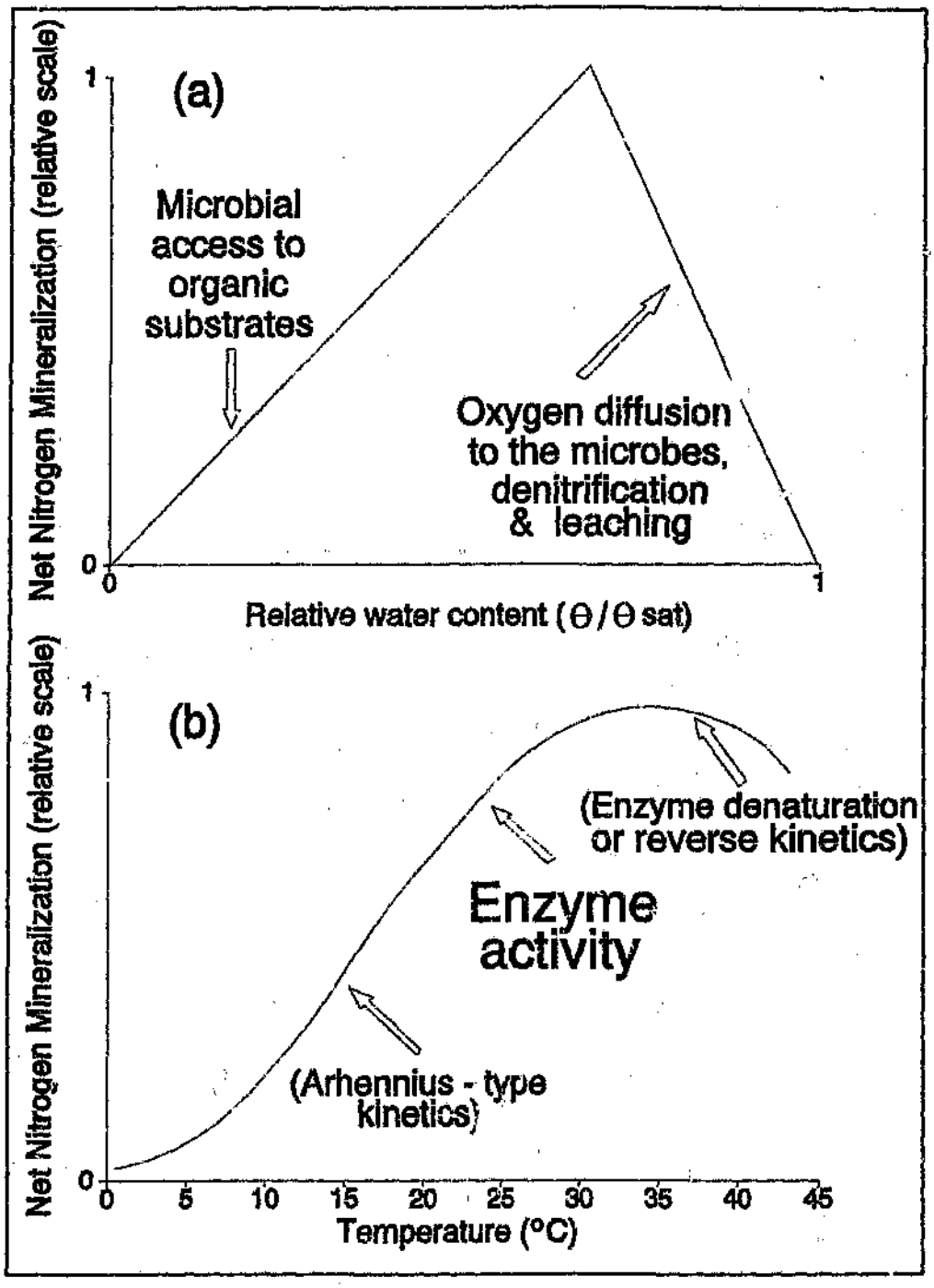


Figure 7.3: Nitrogen mineralization in relation to moisture availability (a) and temperature (b). Annotations describe rate limiting processes.

optimum temperature for nitrification at approximately 35°C and for ammonification a few degrees higher than this (Stanford & Smith 1972). At very high temperatures nitrogen mineralization is progressively inhibited because enzymes are denatured.

7.1.2.4 INTERACTIONS BETWEEN CARBON AND NITROGEN ASSIMILATION

Water availability and temperature are two environmental factors that affect both carbon assimilation and nitrogen mineralization. However, the functional response of these biological processes to these two environmental variables differs.

At low soil water contents, nitrogen mineralization is favoured relative to carbon assimilation since the microbes responsible for mineralization are active at water potentials far below the plant wilting point, where carbon assimilation ceases (Fig. 7.4a). At high soil moisture, nitrogen mineralization is reduced through leaching and nitrification, whereas carbon assimilation is only affected near saturation.

The effect of soil physical characteristics on water availability would indirectly affect nitrogen mineralization. Clay soils yield less water to plants than sandy soils given the same amount of rainfall added to the soil profile. Independent of the effect of soil type on soil nutrient status, clay soils would therefore tend to support sweetveld, particularly in the low to intermediate rainfall areas. In high rainfall areas the effect of soil physical characteristics on moisture availability is overridden by rainfall itself. A further feature of the effect of soil type on moisture conditions that affects nitrogen mineralization is that clay soils have a higher water content than sands below wilting point. Microbial activity at these water potentials would enhance nitrogen mineralization in clays to a greater extent than in sands.

The optimum temperature for carbon assimilation is in the region of 25 to 30°C, whereas for nitrogen mineralization it is typically in the region of 35 to 45°C. At low temperatures, carbon assimilation is favoured relative to nitrogen mineralization (Fig. 7.4b). As the mean daily temperature increases, carbon assimilation and nitrogen mineralization are more closely balanced. Very high temperatures favour nitrogen mineralization relative to carbon assimilation.

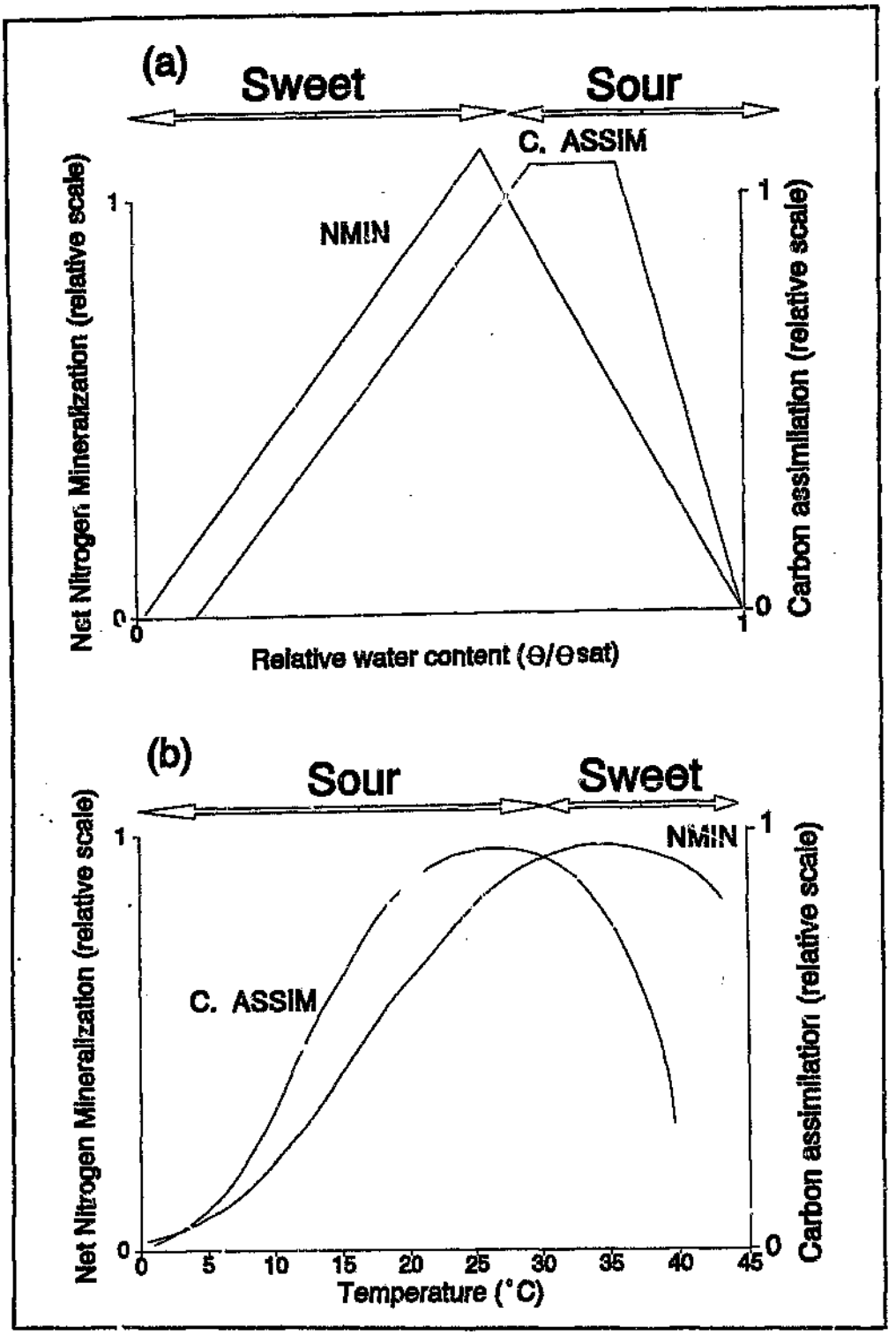


Figure 7.4: An hypothesis of the determinants of sweetveld and sourveld in South Africa. Where carbon assimilation (C. ASSIM) is favoured relative to nitrogen metabolism (NMIN), it is hypothesised that souveld will occur. Where nitrogen metabolism is favoured relative to carbon assimilation sweetveld will occur. The carbon assimilation and nitrogen mineralization curves are presented for moisture availability (a) and temperature (b).

The present model predicts sweetveld in warm, dry areas, or in areas where the parent material gives rise to soils with a high clay content. It predicts sourveld in cool, moist areas, or those with parent material that gives rise to sandy soils. This to a large degree reflects the known distribution of these two vegetation types (cf. Tainton 1981), and provides a mechanistic framework in which to examine not only the observed distribution, but also the seasonal dynamics in forage quality in these two veld types, as well as the response of sourveld to certain manipulations such as burning, grazing or the application of fertilizer.

7.2 METHODS

7.2.1 MACROCLIMATE, GEOLOGY, AND THE DISTRIBUTION OF SWEETVELD, MIXED VELD AND SOURVELD

The relationship between the distribution of sweetveld, mixed veld and sourveld and climate was investigated at the subcontinental scale using the water balance model described in Chapter 4. A total of 170 weather stations in known veld types in the summer rainfall areas based on Tainton (1981) were examined (Fig. 7.5), using the list of climatic indices given in Table 7.1. A stepwise discriminant analysis using forward selection (SAS 1985) was used to investigate the climatic separation of these three vegetation types. The analysis was terminated when the probability of the F-value being exceeded was greater than 0.10. The role of parent material was investigated in cases where stations were not discriminated on the basis of climatic differences.

7.2.2 INVESTIGATING THE IMPORTANCE OF MICROCLIMATE AND SOIL FERTILITY

7.2.2.1 VEGETATION SAMPLING AND SITE DESCRIPTION

At a more detailed scale of resolution, the distribution of sweetveld, mixed veld and sourveld was investigated using the same set of data described in the previous chapter for 101 intensively sampled study sites in the study area. Vegetation sampling, site characteristics, soil sampling, soil analyses and microclimate were the same as those

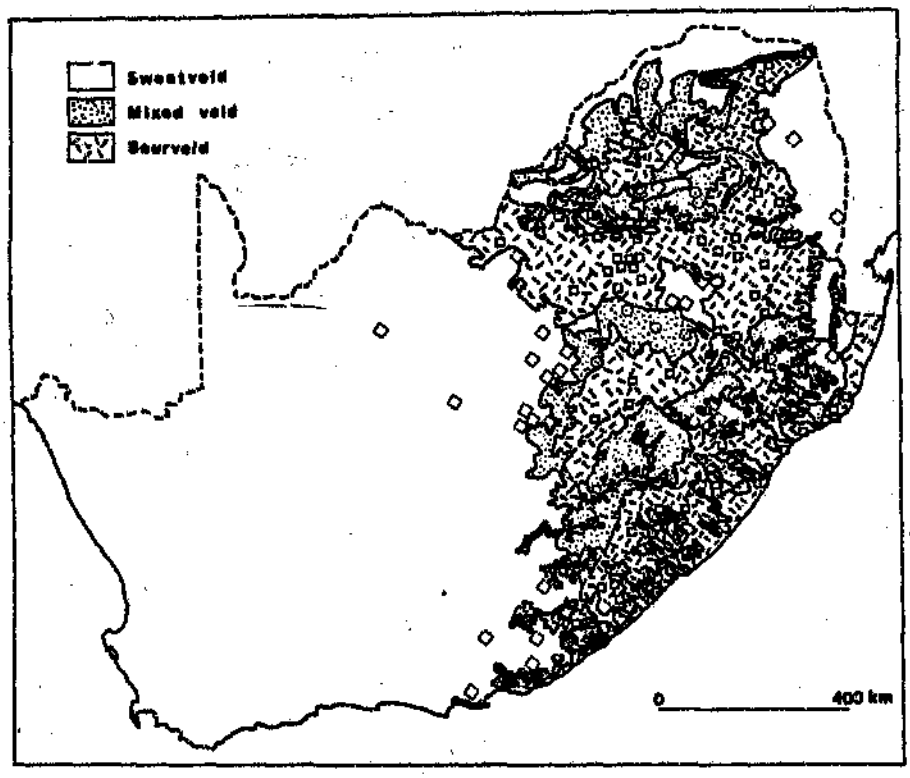


Figure 7.5: The distribution of weather stations in sweetveld, mixed veld and sourveld areas of South Africa (after Tainton 1981).

Table 7.1: Variables included in the stepwise discriminant analysis of climatic differences between sweetveld, mixed veld and sourveld, and the abbreviations for each variable (see text, figures and tables that follow).

VARIABLE	ABBREVIATION
Duration of the growth season	GDAYS
Growth season temperature	GTEM
Non-growth season temperature	NGTEM
Temperature difference between growth and non-growth seasons	TDIF

described in the previous chapter.

7.2.2.2 DATA ANALYSES

It is widely recognised that local sites in one or other of Acocks's (1975) veld types may be very different in terms of their forage quality dynamics and ability to sustain animal production from the regional situation. For example, a site within a veld type classified by Acocks (1975) as sweet, may only sustain animal production for less than six months, and as such be 'sour'. For this reason, each site was classified as sweet, intermediate (mixed veld) or sour based on species composition. Generally, species can be classified into one of these categories on the basis of their palatability at various times of the year, particularly late during the growth season and into the dry season. Species that are unpalatable throughout the year were classified as sour. This information was obtained from the literature (Roberts 1973, Tainton et al. 1976, van Oudtshoorn 1991).

Problems with this approach are that the palatability of a single species may be variable (e.g. Themeda triandra may be classified as sweet, mixed or sour, depending on local conditions; Tainton et al. 1989, Zacharias 1990), and that the palatability of some species is not known. In order to avoid having to classify every species encountered during sampling as sweet, intermediate or sour, species were selected such that the sum of basal covers of the most abundant species was greater than 80% of the total cover in each plot. This reduced the total number of species under consideration from approximately 140 to 62. The classification of species into a palatability class is given in Table 7.2.

A further problem with this approach is that there is no prior indication of what the proportion of sweet or sour species should be in order to classify a site as sweet, intermediate (mixed) or sour. An approach to solving this problem was developed based on the following simple intuitive approach illustrated graphically in Figure 7.6. It was assumed that for a site to be classified as 'sour', it needed an overwhelming contribution of species that were sour, and that the contribution of sweet species had to be small. It was therefore stipulated that of the total cover by species classified according to palatability, at least 60% had to be by species classified as sour, with

Table 7.2: Lists of species classified as sour, intermediate or sweet. The cover of each of these species in study sites was used to classify sites as sour, intermediate or sweet (see text).

SOUR	INTERMEDIATE	SWEET
Alloteropsis semialata	Brachiaria nigropedata	Anthephora pubescens
Andropogon appendiculatus	Brachiaria serrata	Digitaria eriantha
Andropogon schirensis	Digitaria monodactyla	Digitaria tricholaenoides
Aristida adscensionis	Diheteropogon amplectens	Eragrostis obtusa
Aristida bipartita	Eragrostis capensis	Panicum coloratum
Aristida congesta	Eragrostis chloromelas	Paspalum scorbiculatum
Aristida diffusa	Eragrostis curvula	Tetrachne dregei
Aristida junciformis	Eragrostis lehmanniana	
Aristida stipitata	Eragrostis pallens	
Aristida transvaalensis	Eragrostis racemosa	
Cymbopogon plurinodis	Eragrostis stapfii	
Diheteropogon filifolius	Eragrostis superba	
Elionurus muticus	Heteropogon contortus	
Eragrostis gummiflua	Koeleria capensis	
Eragrostis plana	Melinis nerviglume	
Eragrostis sclerantha	Melinis repens	
Eulalia villosa	Microchloa caffra	
Festuca caprina	Monocymbium ceresiiforme	
Festuca costata	Setaria sphacelata	
Harpochloa falx	Themeda triandra	
Hyparrhenia hirta		
Loudetia simplex		
Melica decumbens		
Merxmuellera disticha		
Panicum schlonii		
Rendlia altera		
Schizachyrium sanguineum		
Sporobolus africanus		
Sporobolus fimbriatus		
Sporobolus pectinatus		
Sporobolus pyramidalis		
Trachypogon spicatus		
Triraphis andropogonoides		
Tristachya leucothrix		
Tristachya rehmannii		

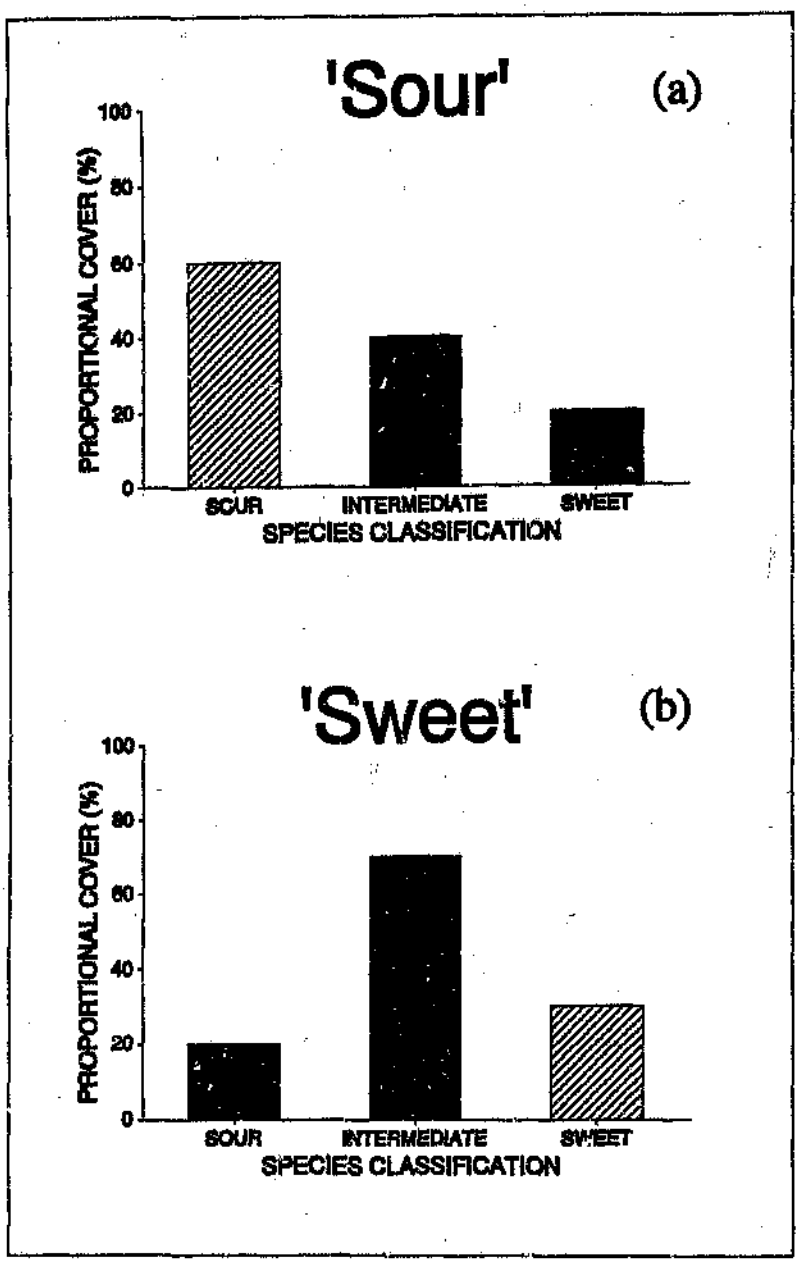


Figure 7.6: Diagrammatic illustration of the scheme used to classify sites as sour (a) and sweet (b) on the basis of the contributions of species classified as sour, intermediate and sweet. Cross hatching indicates the maximum contribution of species of a given palatability, while diagonal lines indicate the minimum contribution.

a maximum cover by species classified as sweet being 20%. For a site to be 'sweet' it was assumed that the contribution of sour species had to be relatively small, but that stock would not lose condition even with relatively low cover by sweet species. A site was therefore classified as sweet if it had greater than 30% of its total cover by species classified as sweet provided that the cover by sour species was less than 20%. Sites not classified as sour or sweet based on these criteria were classified as intermediate.

A stepwise discriminant analysis was used as described above to identify climatic and edaphic variables of particular importance. The same environmental variables described to supplement the ordination of stands and species in the previous chapter (cf. Table 6.1) were included in this analysis. The analysis was terminated when the probability of the F-value being exceeded was greater the 0.10.

7.3 RESULTS

7.3.1 DISCRIMINATION OF VEGETATION TYPES AT SUBCONTINENTAL SCALE: THE ROLE OF MACROCLIMATE AND PARENT MATERIAL

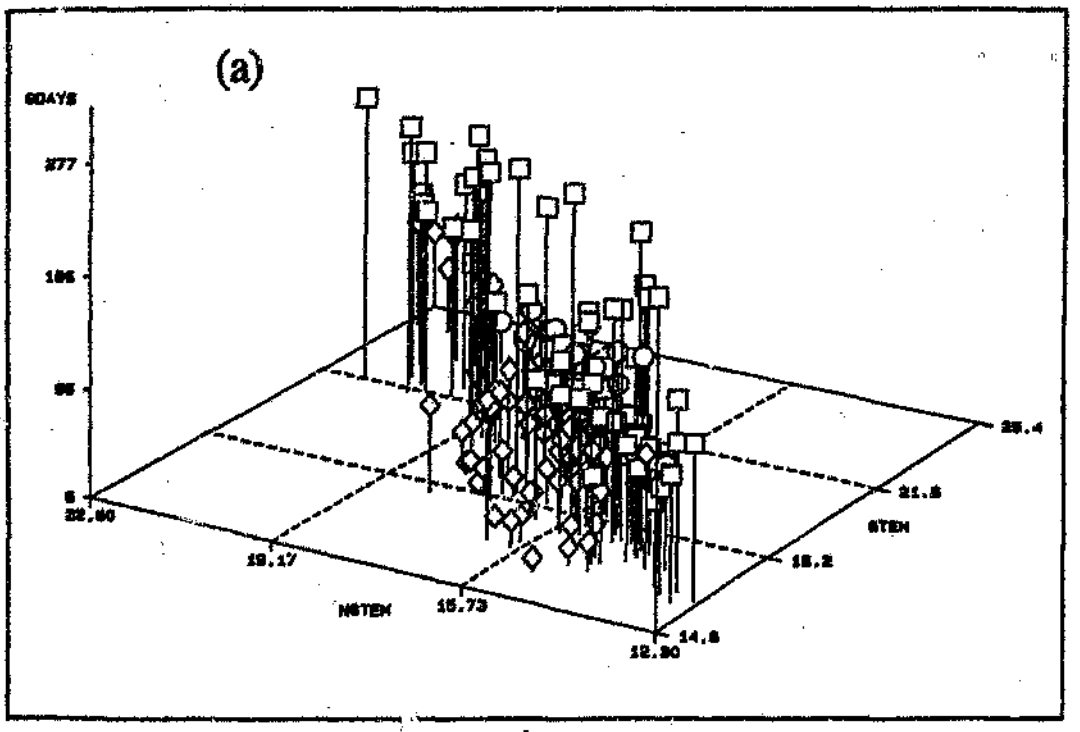
The distribution of sweetveld, mixed veld and sourveld is partly related to climate. The climatic variables included in the discriminant analysis output, and their order of inclusion, indicate that the duration of the growth season (GDAYS) and the temperature difference between the growth and no-growth seasons (TDIF) are significant ($P<0.05$; Table 7.3). The distribution of weather stations in relation to the duration of the growth season (GDAYS), and the temperature indices from which the variable TDIF was derived (the growth season temperature (GTEM) and the no-growth season temperature (NGTEM)) gives a better impression of the importance of water availability and temperature in discriminating these vegetation types than does the plot of the two former indices (GDAYS and TDIF) on their own. Sourveld experiences greater water availability than sweetveld (Fig. 7.7a). Mixed veld occurs in regions of intermediate water availability. Rainfall in mixed veld and sourveld is more strongly seasonal than in sweetveld (Fig. 7.7b).

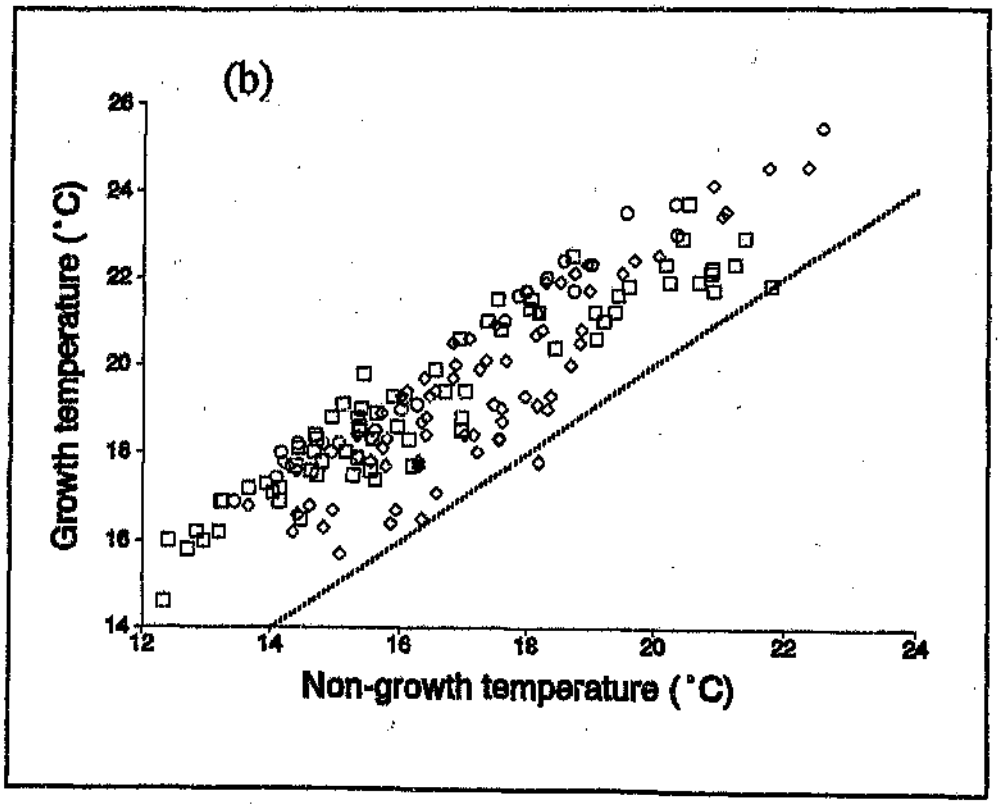
The overall climatic differences between sweetveld, mixed veld and sourveld are

TABLE 7.3: A summary of the stepwise discriminant function analysis based on forward selection, showing the order of inclusion of each climatic variable in the present attempt to discriminate sweetveld, mixed veld and sourveld. The order of inclusion (STEP), partial correlation coefficients (PARTIAL R-SQUARED), F-statistic (F-STAT) and probability of exceeding F (PROB > F) are included. The analysis was stopped at probability > F being 0.10.

STEP	VARIABLE ENTERED	PARTIAL R-SQUARED	F-STAT	PROB > F
1	GDAYS	0.546	64.8	.0001
2	TDIF	0.248	19.9	.0001

Figure 7.7: The distribution of weather stations in sweetveld (◇), mixed veld (○) and sourveld (□) areas; (a) in relation to the temperature during the growth season (GTEM) and the no-growth season (NGTEM), and the duration of the growth season (GDAYS), and (b) in relation to the temperature during the growth season (GTEM) and the no-growth season (NGTEM). The line joining points of equal temperature of the temperature plane is the line of zero seasonality of rainfall.


(a)
GDAYS
277
186
95
5
22.80
19.17
NSTEM
15.73
12.30
14.6
18.2
21.8
25.4
STEM


(b)
Growth temperature (°C)
Non-growth temperature (°C)
26
24
22
20
18
16
14
12
14
16
18
20
22
24

summarised in Figure 7.8. Sourveld experiences a significantly greater ($P<0.01$) number of growth days per annum than sweetveld. Significant differences ($P<0.01$) between these two vegetation units and mixed veld based on the difference in temperature between the growth and no-growth seasons are also evident. Mixed veld is intermediate both in terms of the duration of the growth season and the temperature in the non-growth season, but has higher values than both sweetveld and sourveld in respect of the growth season temperature and the difference in temperature between the growth and no-growth seasons. If mixed veld is intermediate - as is widely accepted - then it would seem to be the duration of the growth season and/or the temperature during the no-growth season that contributes most to the distribution of these vegetation types.

The distribution of weather stations in sweetveld, mixed veld and sourveld in relation to the duration of the growth season (GDAYS) and the difference in temperature between the growth and no-growth temperatures (TDIF), is illustrated in Figure 7.9. As the difference between the growth and no-growth temperatures increases (as rainfall becomes more strongly seasonal), the number of growth days required for sourveld decreases. All of the climate stations in sourveld occur above the negative exponential curve indicated in Figure 7.9a and the majority (74.2%) of stations in sweetveld occur below this curve. This curve can therefore be considered to represent the minimum water availability - rainfall seasonality conditions of sourveld. It also appears that all of the stations in sweetveld occur in situations with fewer than 120 growth days per annum. Mixed veld occurs in areas that climatically tend to support sourveld. Closer scrutiny of the moisture - rainfall seasonality plane (Fig. 7.9b) provides some indication that soil fertility may play a role in determining the distribution of sweetveld and sourveld. Weather stations in sweetveld which occur in areas that climatically appear suitable for sourveld have soils derived from basic volcanic parent material (Table 7.4). This is illustrated by the distribution of a patch of sweetveld in the highveld of the south-eastern Transvaal, which climatically is expected to support sourveld (Fig. 7.10a). However, the distribution of dolerite closely matches the distribution of sweetveld in this area, suggesting a relationship between the two (Fig. 7.10b). Use of a geological rather than a soils map for this purpose is not ideal - particularly where the geology is as fragmentary as this. A similar relationship between the substratum geology and the distribution of sweetveld

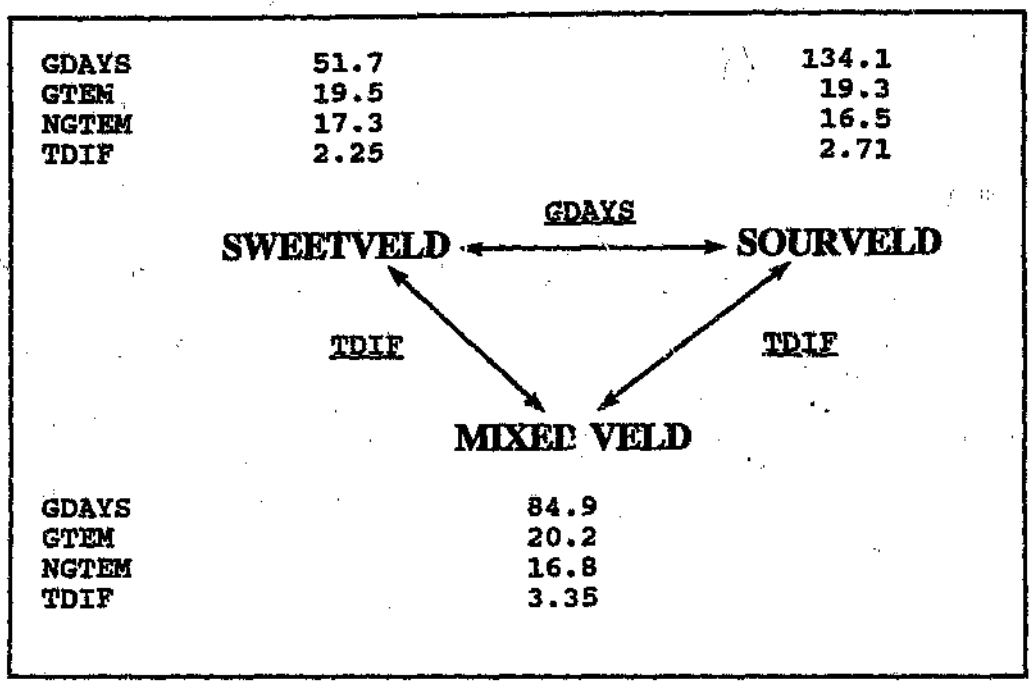


Figure 7.8: Mean values for each of four climatic variables for weather stations in sweetveld, mixed veld and sourveld. Statistically significant mean values ($P<0.05$) are indicated by the underlined variable names (between vegetation type names).

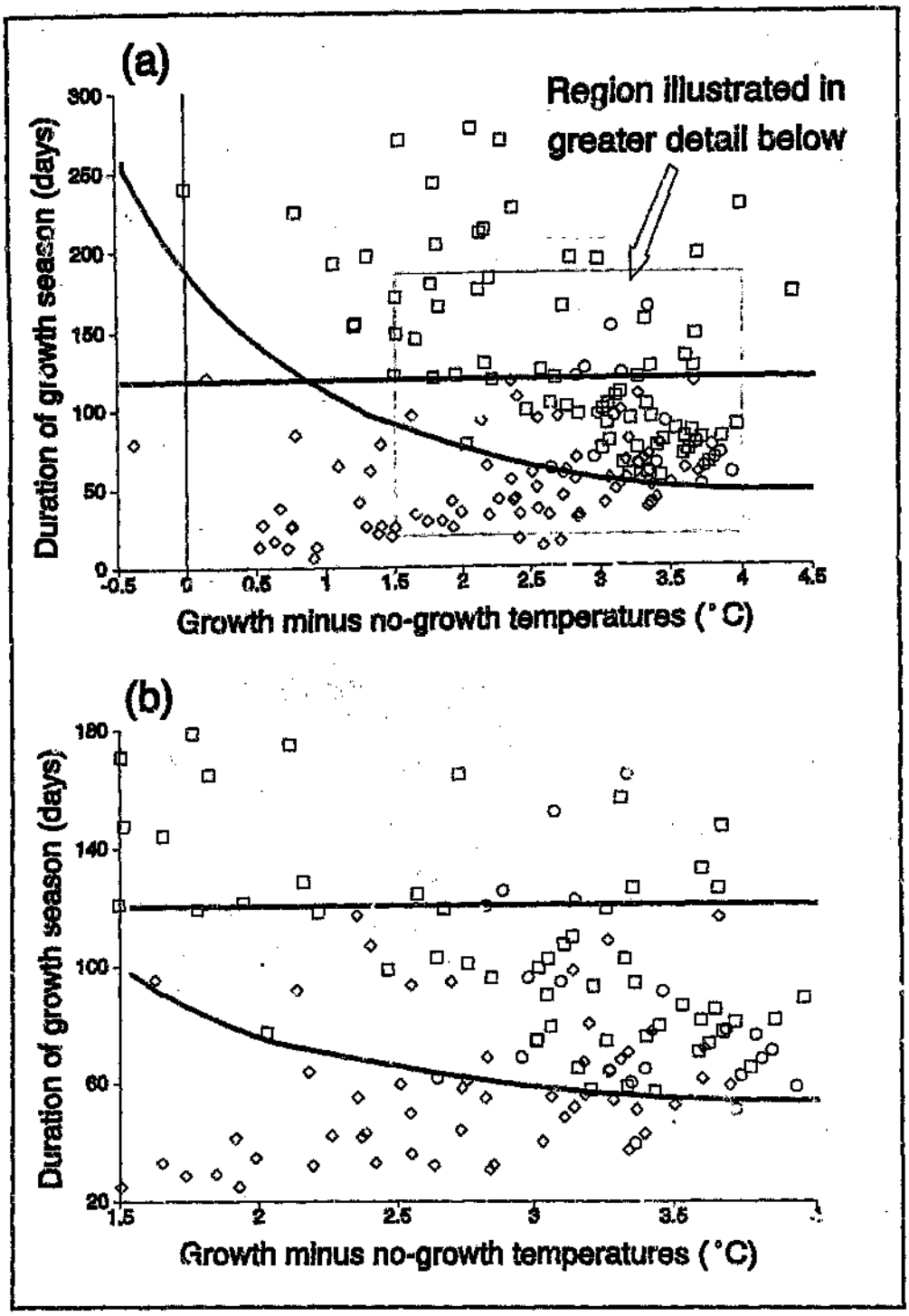


Figure 7.9: The distribution of weather stations in sweetveld (◇), mixed veld (○) and sourveld (□) areas in relation to the growth minus the no-growth temperature (an index of the degree of seasonality of rainfall) and the duration of the growth season. All stations used in the study are illustrated in (a) and the region of overlap in sweetveld, mixed veld and sourveld is shown in greater detail in (b).

Table 7.4: The parent material of stations that were mapped as sweetveld (Tainton 1981), but that were predicted as being sourveld on the basis of climate (cf. Fig. 7.9).

PARENT MATERIAL	NUMBER OF STATIONS
Intermediate (andesite, granite, karoo sediments)	6
Intermediate, but with extensive basic volcanics in vicinity	5
Basic (basalt, dolerite, gabbro, norite)	10

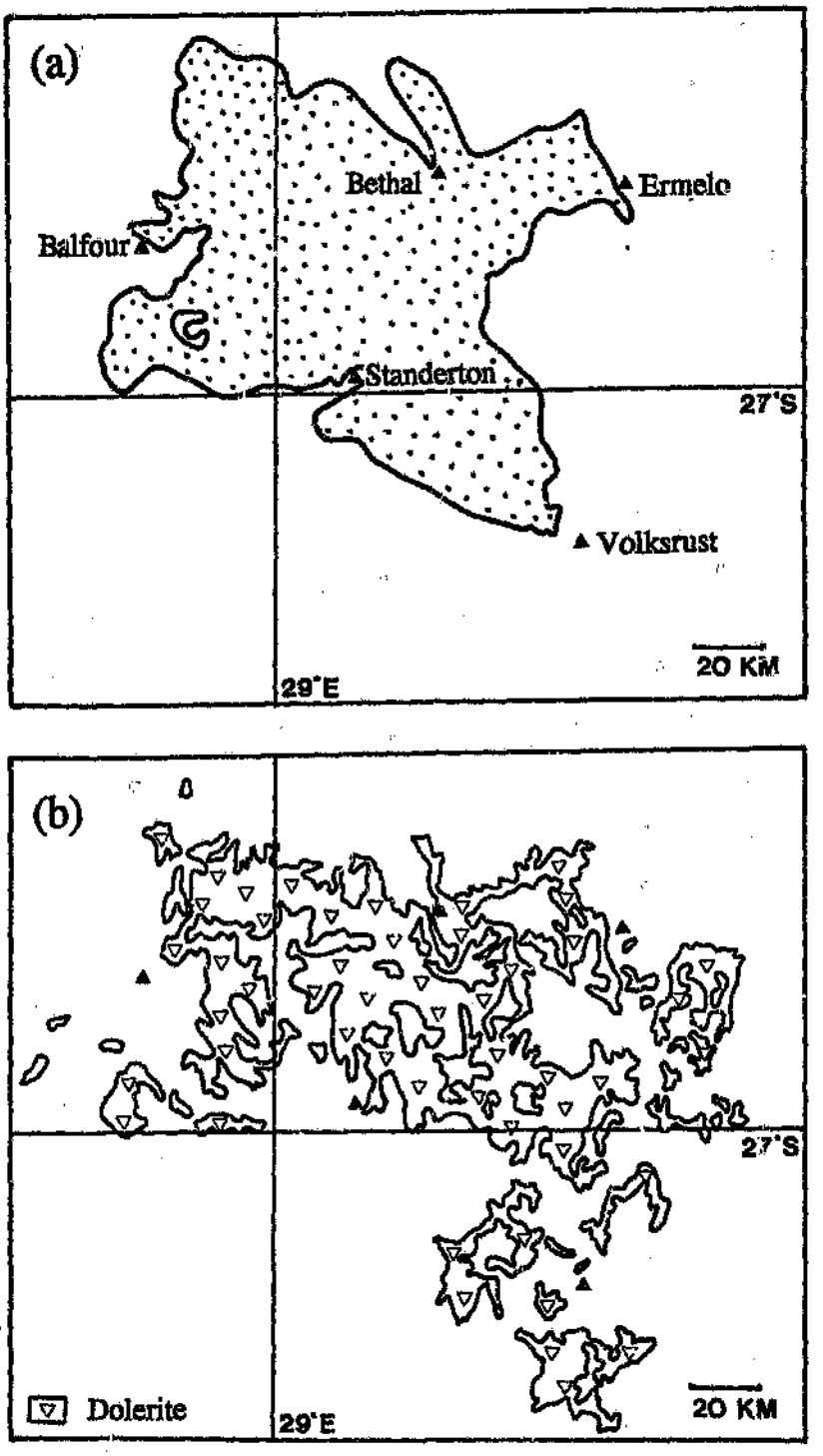


Figure 7.10: The relationship between the distribution of a patch of sweetveld in the south-eastern Transvaal (a) and the distribution of dolerite within an area of karoo sediments (b). Based on climate, this area of sweetveld would be expected to support sourveld.

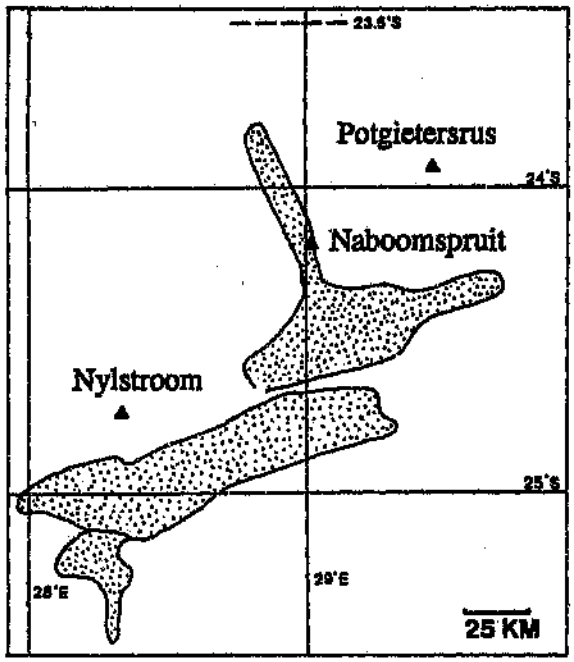
in the northern Transvaal further illustrates the relationship between the presence of basic rocks (basalt and norite/gabbro) and the distribution of sweetveld (Fig. 7.11a,b).

7.3.2 THE ROLE OF SOIL NUTRIENTS

The combined analysis of microclimate, parent material and soil fertility of sites classified as sour, intermediate or sweet on the basis of species composition, illustrates the determinants of the distribution of these grassland types more clearly than the subcontinental scale analysis. Based on the analysis of the distribution of these vegetation types in relation to the same climatic variables, as well as on the basis of parent material (cf. previous section), it is possible to predict whether each of the study sites is sweet, mixed or sour. All of the sites classified as sweet were correctly predicted. Nine of the 39 sites classified as sour were predicted as sweet. Of these, three were on soils derived from basic parent material. These sites had all been heavily grazed. The remaining six sites were on sandstones or quartzites. Of the sites classified as intermediate, but that were incorrectly predicted as being sweet, three were on soils derived from basic parent material. Once again, these had all been heavily grazed. A further 16 sites classified as intermediate were incorrectly predicted as sweet. Ten of these were on soils derived from parent material of intermediate base status, and the remaining six were on soils derived from acidic parent material.

These data highlight shortcomings of the subcontinental scale analysis; that sourveld occurs on soils derived from sandstones or quartzites, and that mixed veld occurs on soils derived from parent material of intermediate or low base status, irrespective of climate. The absence of extensive outcrops of acidic or intermediate parent material (mappable at the subcontinental scale) in areas that climatically appear to support sweetveld, resulted in the easy identification of the negative exponential curve indicating the lower limit of sourveld distribution on the subcontinental scale analysis.

In addition to the climatic variables identified at the subcontinental scale, namely the duration of the growth season and the difference in temperature between the growth and no-growth seasons, particular aspects of soil fertility were also recognised as important in discriminating sweetveld, mixed veld and sourveld. Extractable



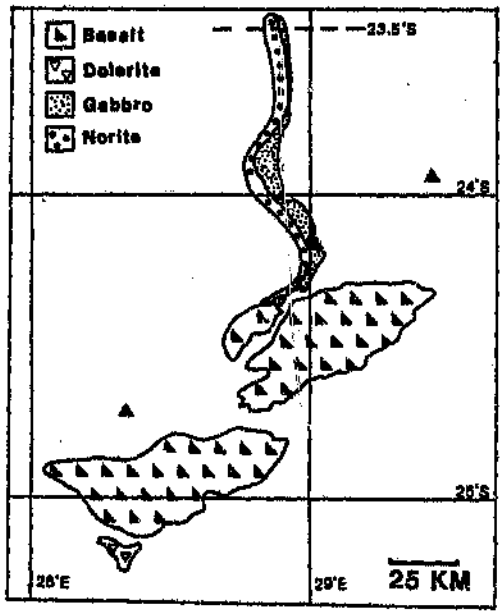


Figure 7.11: The distribution of a patch of sweetveld (a) in the central Transvaal and the distribution of basic igneous rocks (b). Based on climate this area of sweetveld would be expected to support sourveld.

phosphorus (PO4) and the size of the readily mineralizable nitrogen pool (NMIN) are correlated to the distribution of sites classified as sweet, intermediate and sour (Table 7.5). The final variable entered in the stepwise discriminant analysis ($P<0.10$) was the sum of calcium, magnesium and potassium in the B-horizon (CMKB).

The distribution of sweet, intermediate and sour sites in relation to moisture availability (GDAYS), the concentration of available phosphorus (PO4) and the index of mineralizable nitrogen (NMIN) is striking (Fig. 7.12). There is increasing sourness with an increase in both the duration of the growth season and the size of the readily mineralizable nitrogen pool, and with decreasing phosphorus availability.

7.3.3 PREDICTING THE DISTRIBUTION OF SWEETVELD, MIXED VELD AND SOURVELD

Sweetveld, mixed veld and sourveld discriminate reasonably well at the broad-scale based on climate and parent material. Sourveld occurs in areas of high moisture availability relative to the difference in temperature between the growth and no-growth seasons, on soils derived from parent material of intermediate or low base status (Fig. 7.13). It also occurs on soils derived from quartzites or sandstones at low moisture availability. Sweetveld occurs in arid areas relative to the difference in temperature between the growth and no-growth seasons, on soils derived from parent material of intermediate or high base status. It also occurs on soils derived from basic igneous rocks such as basalt, dolerite, norite or gabbro in more mesic areas. Mixed veld is considered intermediate between sweetveld and sourveld, both in terms of its forage quality dynamics and the determinants of its distribution.

The scheme is very successful for sweeteld as well as sourveld at a broad (subcontinental) scale, with all of the weather stations in these vegetation types predicted correctly by the decision tree depicted in Figure 7.13. Stations in mixed veld occur in areas with similar climate to sourveld, but on soils with a higher base status. It is difficult to test the model for local study sites, because of problems associated with the classification of sites based on species composition. Ideally such a model should be developed empirically, and incorporate microclimatic influences and particular soil nutrients such as phosphorus and nitrogen.

Table 7.5: Summary of the stepwise discriminant analysis based on forward selection of study sites classified as sweet, intermediate (mixed) and sour. A total of 17 environmental variables were included in the analysis, of which 5 were entered with a probability of less than 0.10. The order of inclusion (STEP), partial correlation coefficients (PARTIAL R-SQUARED), F-statistic (F-STAT) and probability of exceeding F (PROB > F) are included.

STEP ENTERED	VARIABLE	PARTIAL R-SQUARED	F-VALUE	PROB>F
1	PO4	0.325	23.6	0.0001
2	GDAY	0.116	6.4	0.0025
3	NMIN	0.199	11.9	0.0001
4	TDIF	0.132	7.2	0.0012
5	CMKB	0.050	2.5	0.0894

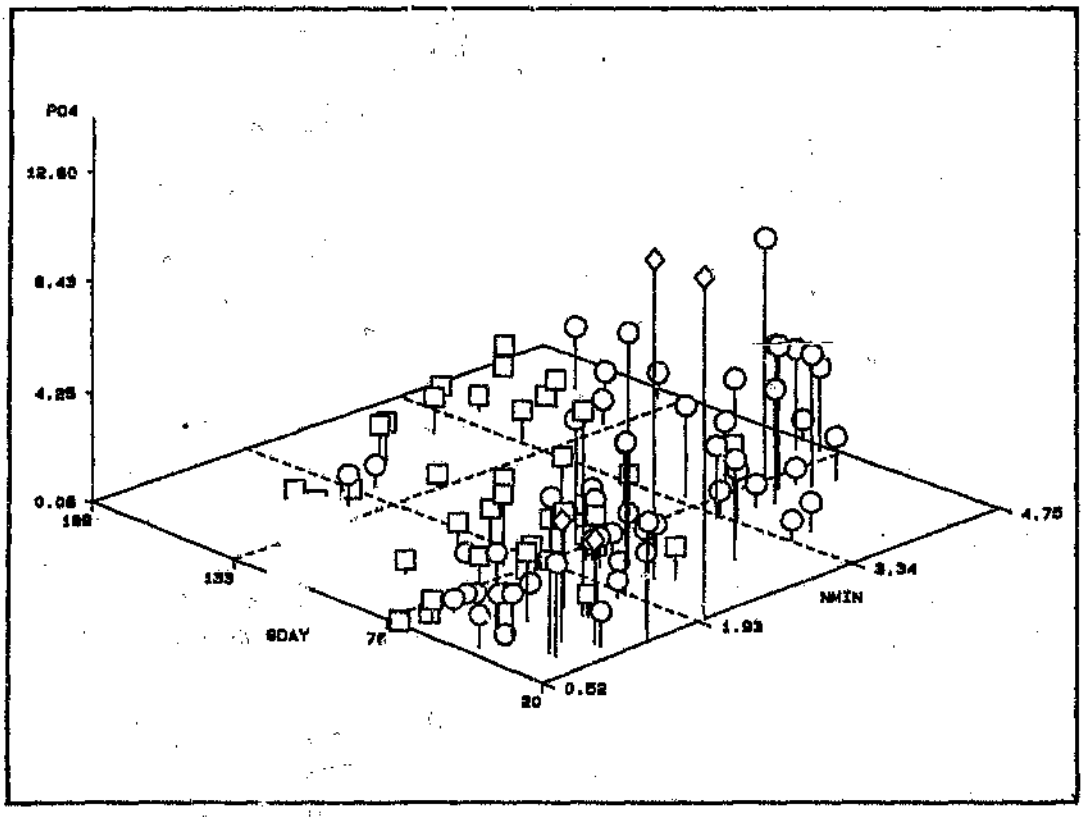


Figure 7.12: The distribution of stands in the grassland biome classified on the basis of species composition as sweetveld (◇), mixed veld (○) and sourveld (□) in relation to the duration of the growth season (GDAYS), resin bag extractable phosphorus (PO4) and size of the readily mineraliable nitrogen pool (NMIN).

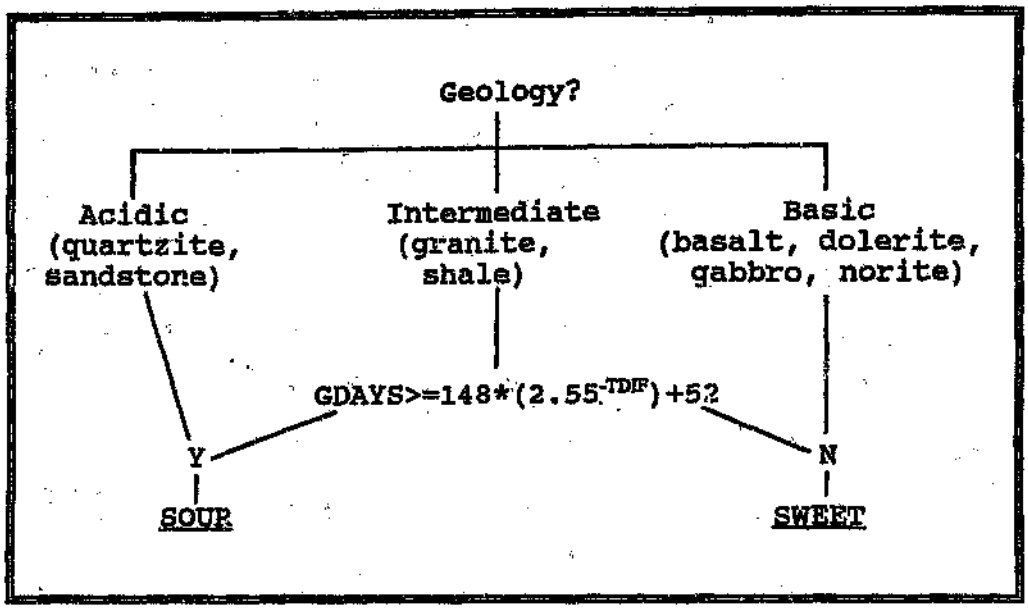


Figure 7.13: A decision tree predicting the distribution of sweetveld and scurveld in relation to geology and climate. Mixed veld is considered intermediate, and has not been well discriminated in the present study.

7.4 DISCUSSION

7.4.1 THE CARBON/NUTRIENT BALANCE AND THE DISTRIBUTION OF SWEETVELD AND SOURVELD

The duration of the growth season is a useful indicator of plant productivity and is therefore a good index of carbon assimilation, particularly where temperature is not limiting during the season when moisture is available, as in the grassland biome (cf. Chapter 4). The nutrient index of phosphorus availability decreases with increasing sourness (Table 7.6), which is what might be expected. Both of these trends support the resource availability hypothesis (Bryant et al. 1983, Coley et al 1985). However, the size of the readily mineralizable nitrogen pool increases with increasing sourness (Table 7.6), apparently contradicting the resource availability hypothesis. It may not be the values of these indices *per se* that are important in the discrimination of sweetveld, mixed veld and sourveld, but rather their relationship to indices of carbon assimilation (cf. Bryant et al. 1983). If the nutrient indices are expressed as a fraction of carbon assimilation (the duration of the growth season), values increase from sweet to mixed to sour sites for both available phosphorus and the readily available nitrogen pool (Table 7.6), reflecting increased carbon assimilation relative to nutrient availability with increasing sourness. Sourness is therefore related to the degree to which the environment promotes carbon assimilation relative to nutrient mineralization and assimilation.

Although the present study suggests that phosphorus is important in determining the distribution of sweetveld and sourveld, the effects of nitrogen and phosphorus may not be independent. The dynamics of phosphorus in base-poor soils are similar to those of nitrogen, in that the main soil pool is organic phosphorus which must be released by biological mineralization (Coleman et al. 1983). If this is the case the dynamics of nitrogen and phosphorus in the soil-plant system are likely to be similar. Alternatively, rates of nitrogen mineralization may be limited by phosphorus availability (Purchase 1974). If this is the case, the role of phosphorus in determining the distribution of sweetveld and sourveld may be indirect, via control on nitrogen availability.

Table 7.6: Indices of carbon assimilation (duration of the growth season) nutrient availability (available phosphorus and the size of the readily mineralizable nitrogen pool), and nutrient indices as a fraction of an index of carbon assimilation in sites classified as sour, intermediate and sweet.

VARIABLE	SOURVELD	INTERMEDIATE	SWEETVELD
Index of carbon availability (GDAYS)	102.6	72.6	33.4
Available phosphorus (PO4)	1.34	2.21	8.23
Size of mineralizable nitrogen pool (NMIN)	2.18	2.67	1.63
GDAYS/PO4	152.1	88.15	5.24
GDAYS/NMIN	54.1	32.7	22.4

7.4.2 TOWARDS A MECHANISTIC MODEL

A mechanistic model illustrating the driving variables and biological processes that determine forage quality is illustrated in Figure 7.14. The relative balance of carbon assimilation and nitrogen mineralization at a site determines its forage quality. Temperature and moisture availability are emphasised in that they affect both nitrogen mineralization and carbon assimilation directly. Two additional variables, radiant flux density and the carbon dioxide concentration of the atmosphere affect carbon assimilation. Soil characteristics, including the clay content and clay type affect nitrogen mineralization, both through their effect on water availability and the degree to which organic matter is protected in the soil. There is a feedback in that herbage quality affects litter quality, and thus soil nutrient status (cf. Ellis 1990).

The model provides a useful basis for predicting the response of South Africa's grassland types to global increases in atmospheric carbon dioxide concentration. The increase in carbon assimilation relative to nutrient assimilation given this scenario is likely to decrease forage quality overall in South Africa's grasslands (Couteaux et al. 1991) and may lead to the expansion of sourveld at the expense of sweetveld and mixed veld. However, an increase in temperature or a decrease in rainfall that may accompany the increase in atmospheric carbon dioxide (Schneider 1992) would have the opposite effect. The model requires detailed calibration before the impact of scenarios of climate change can be investigated for these vegetation types.

In contrast to the suggestion in a number of studies, that forage quality declines with decreased light availability (Bryant et al. 1983, Coley 1983, Coley et al. 1985, Bazzaz et al. 1987, Chapin et al. 1987), the present model predicts an increase in forage quality with decreased light intensity. Past models have emphasised potential growth rates of plants adapted to survive in different environments as determining their strategy to cope with herbivory (Grime 1977, Coley et al. 1985, Chapin et al. 1987), and have suggested that in stressful environments such as those that experience low light availabilities, plants grow slowly and therefore take up small quantities of nutrients. The present study emphasises the relative ability of the environment to promote carbon assimilation relative to nutrient mineralization and assimilation. Since carbon assimilation is related to light intensity, whereas nutrient availability is

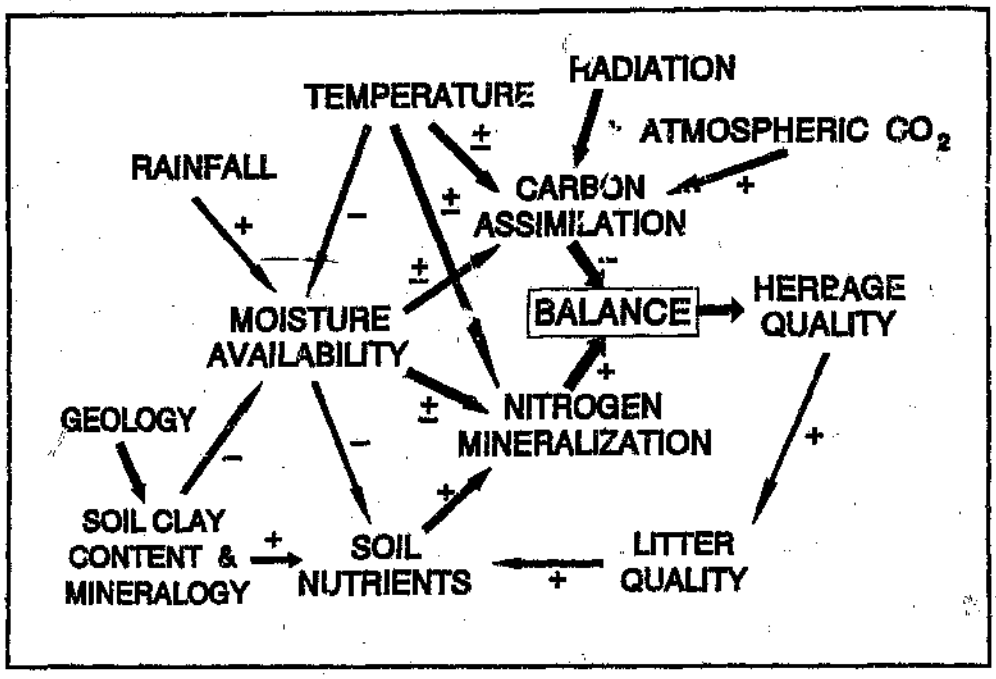


Figure 7.14: A conceptual model illustrating the determinants of grass forage quality within the grassland biome. Forage quality is considered to be determined by the relative tissue concentrations of carbon and nitrogen. The determinants of carbon assimilation and nitrogen mineralization are emphasised, with positive and negative symbols indicating the effect of increasing the value of a variable on carbon and nitrogen assimilation, and hence on herbage quality.

independant of light availability (cf. Fig. 7.14), shading would be expected to reduce carbon assimilation to a greater extent than nutrient mineralization and assimilation, leading to an increase in forage quality. At least, plants growing in these environments would not be expected to have carbon based defences such as tannin or high fibre contents.

7.4.3 IMPLICATIONS FOR THE SEASONAL CYCLE OF NITROGEN AND CARBON ASSIMILATION IN NATURAL GRASSLANDS

The sequence of events at the onset of the wet season through to the dry season are described for wet and dry areas respectively, in order to explain how the model predicts seasonal forage quality dynamics. Soil is wetted at the beginning of the growth season. Carbon assimilation is limited by a low leaf area. Leaf expansion and growth requires several weeks, or in the case of reactivation of severely wilted leaves, several days. In contrast, nitrogen mineralization responds to wetting within minutes to hours. Plant tissue produced early in the growth season is therefore rich in nitrogen relative to carbon, and of high forage quality. In wet areas the readily mineralizable pool of nitrogen becomes exhausted as the season progresses, and nitrogen mineralization declines. At this stage, the plants have a high leaf area, and in the absence of moisture stress, carbon assimilation continues. Plant tissue therefore becomes progressively more carbon rich and nutrient poor (sour) during the wet season in moist areas, remaining so into the dry season when physiological activity ceases.

In arid areas rainfall is erratic, and the soil is wet in discrete episodes. Microbial mineralization responds to wetting within hours, while carbon assimilation must wait on rehydration and/or regrowth of green leaf tissue. It seems that the mineralizable pool is not exhausted prior to the following rainfall event, by which time the soil may or may not have dried sufficiently for either carbon assimilation or both carbon assimilation and nitrogen mineralization to have declined. In either case, wetting would result in a similar rapid nitrogen mineralization response and slower carbon assimilation response as described for the beginning of the wet season. Furthermore, the system spends more of its time in the water limited state, which favours nitrogen mineralization over carbon assimilation due to the lower water requirement for

nutrient mineralization than photosynthesis. The general combination in the grassland biome of wet and cold, and hot and dry, (Mentis & Huntley 1982), favours carbon assimilation over nutrient mineralization, and nutrient mineralization over carbon assimilation respectively, accounting for the occurrence of sourveld and sweetveld respectively in these areas.

7.4.4 THE EFFECT OF CERTAIN MANIPULATIONS ON FORAGE QUALITY IN SOURVELD

Any manipulation that increases nutrient supply relative to carbon assimilation will lead to an increase in forage quality. The observed increase in forage quality following heavy grazing or mowing is due to a reduction in carbon assimilation by reducing the leaf area, and possibly an increase in nitrogen mineralization due to root turnover, dunging and urination. Similarly, following fire, sourveld is more palatable and nutritious than at other times. By removing standing leaf material, carbon assimilation decreases due to a reduced leaf area. Despite causing a small overall loss of nutrient capital, fire also results in a flush of potentially mineralizable nutrients (Tainton & Mentis 1984, Christensen 1987). Furthermore, soil temperatures increase and soils tend to dry out following fire (Mentis & Tainton 1984), both favouring nitrogen mineralization over carbon assimilation. The increase in forage quality in sourveld areas following the application of fertilizer can similarly be explained by increased nutrient availability relative to carbon assimilation.

7.5 SUMMARY

An hypothesis has been developed to explain the distribution of sweetveld and sourveld in South Africa. It is based on the resource availability hypothesis, which has traditionally been applied to woody plants and browsers. It is proposed that where carbon assimilation is high relative to nitrogen mineralization and assimilation, plant tissue will have a high carbon to nitrogen ratio, and forage quality will be low (sour). Where nitrogen mineralization is high relative to carbon assimilation, plant tissue will have a low carbon to nitrogen ratio, and sweetveld will occur. Mixed veld is considered intermediate between these two extremes.

While the hypothesis has been developed for carbon and nitrogen asimilation in particular, other organically bound nutrients could be included because their dynamics in the soil-plant system are likely to be similar to that of nitrogen.

Environmental factors that affect carbon assimilation are temperature, water availability, radiant energy and atmospheric carbon dioxide concentration. Radiant energy and the concentration of carbon dioxide in the atmosphere are treated as constant for the grassland biome as a whole. Nitrogen mineralization is also a function of temperature and water availability, as well as the size of the readily mineralizable nitrogen pool. The size of the readily mineralizable pool is related to the amount and nature of organic matter in the soil, which depends on the balance between production and decay. Ultimately the amount of organic matter which a soil can accumulate is set by the degree to which organic matter is chemically or physically protected in the soil. This is determined by soil properties, including clay content and mineralogy. Soil organic matter is stabilised by clays, whereas sandy soils tend to have low organic matter contents, and therefore low total nitrogen.

Water availability and temperature affect carbon assimilation and nitrogen mineralization in different ways. Microbes that are responsible for mineralizing the available nitrogen pool in the soil are able to function at moisture availabilities lower than wilting point, and they respond to wetting almost immediately. Carbon assimilation requires that soil water content be greater than wilting point, and it requires the regrowth of green tissue at the beginning of the wet season in order to utilise available water. The temperature optimum for carbon assimilation is between 25 and 30°C, while that for nitrogen mineralization is in the region of 40°C. At low temperatures carbon assimilation is favoured relative to nitrogen mineralization. As temperatures increase, the two processes are increasingly balanced, until at high temperatures, nitrogen mineralization is favoured relative to carbon assimilation.

The hypothesis explains the known distribution of sweetveld and sourveld, and was tested at two scales of resolution, the subcontinental scale and the local scale. Differences between the distribution of sweetveld, mixed veld and sourveld were related in a general way to climatic and edaphic differences, and more particularly to moisture availability, the degree of seasonality of rainfall, and the base status of

parent material from which soils are derived. Sweetveld is restricted to areas where moisture availability is lower and rainfall is less seasonal than mixed veld and sourveld. It also occurs on soils derived from basic parent material, with increasing sourness associated with increasing acidity of the parent material. Available phosphorus and the amount of mineralizable nitrogen are particular aspects of soil fertility that affect the distribution of these grassland types. It is not known whether the effect of phosphorus on forage quality is direct, or through its regulation of microbial activity and therefore nitrogen mineralization.

A qualitative mechanistic model has been developed that outlines the environmental determinants of forage quality in South Africa's grasslands. It has been used as a basis for describing the seasonal forage quality dynamics in sweetveld and sourveld, and also to explain why sourveld becomes sweeter following certain manipulations. Any manipulation that reduces carbon assimilation relative to nitrogen mineralization, such as heavy grazing, burning and fertilization, tends to improve forage quality.

CHAPTER 8

SYNTHESIS

8.1 A SUMMARY OF THE STUDY

8.1.1 CLIMATE, FIRE, TOPOGRAPHY AND GRASSLANDS

In contrast to past models of the distribution of the grassland biome in South Africa, which have emphasised just one or two primary determinants, the model developed in this study emphasises the combination of a package of environmental conditions necessary for the occurrence of the grassland biome. The combined effects of climate and fire are the primary abiotic environmental factors determining the distribution of South Africa's grasslands. The salient features of a grassland climate are that it has moderate rainfall which is strongly concentrated in summer, and that it has cold winters. Aspects of this climate have been linked to the distribution of grasslands for some time (Weaver & Clements 1938, Borchert 1950, Acocks 1953, Thornthwaite 1952), but only recently have these climatic features been linked to the occurrence of fire (Axelrod 1985, Stephenson 1990). Moderate rainfall in the season in which temperatures are favourable for plant growth enables the accumulation of sufficient fine fuels to carry a fire reasonably frequently. Desiccation of these during the cold, dry season promotes fire.

Three additional climatic features may promote frequent burning in South Africa's grasslands. Firstly, frost cures the sward early in the dry season giving rise to a prolonged dry season. Secondly, lightning strike density is higher in the grassland biome than in any other of South Africa's biomes (Edwards 1984, Manry & Knight 1986). This would have been an important ignition source prior to human settlement. Thirdly, the occurrence of hot, dry winds over much of the eastern seaboard during the winter months, desiccates fuels sufficiently to enable fires.

A further two conditions are necessary for the widespread occurrence of grasslands given a climate conducive to frequent burning. Firstly, a topography that is gently undulating and unbroken and therefore enables fires to spread over large areas is a

necessary part of the grassland environment. Secondly, low to moderate levels of herbivory that do not continuously diminish the standing crop such that fire is excluded or of reduced intensity are a prerequisite. A gently rolling topography is characteristic of the area occupied by the grassland biome, generally being on ancient land surfaces which only on the eastern seaboard show any degree of incision (Partridge & Maud 1987). The incised areas are generally warmer and drier than the undulating interfluves (Tainton 1981), and support savanna (Rutherford & Westfall 1986). Incomplete herbivory is ensured in large parts of the grassland biome, by the unpalatability of grasses during the winter months, and promotes frequent burning (see following section).

8.1.2 DETERMINANTS OF THE DISTRIBUTION OF SWEET AND SOUR GRASSLAND TYPES

The most fundamental distinction between grassland types in South Africa is between sweetveld, mixed veld and sourveld. It is related to seasonal variations in forage quality, and their effects on animal performance. Animal mass gain is sustained throughout the year on sweetveld, for between 6 and 11 months on mixed veld, and for less than 6 months on sourveld.

The distribution of these grassland types is proposed to be due to the balance between carbon and nitrogen assimilation in grassland plants. Nitrogen assimilation is limited in natural systems by the rate of microbial mineralization of nitrogen in the soil. Where carbon assimilation is high relative to nitrogen mineralization, plant tissue has a high carbon to nitrogen ratio and is poor quality forage (sourveld). Sweetveld occurs where nitrogen mineralization is high relative to carbon assimilation. Mixed veld is intermediate between these two extremes.

Climate and soils are the primary determinants of the distribution of these grassland types through their effects on the balance between carbon and nitrogen assimilation in grassland plants. Water availability and temperature influence carbon assimilation and nitrogen mineralization in different ways. The microbes responsible for nitrogen mineralization are active at soil water potentials lower than plant wilting point. At low water availability nitrogen mineralization is favoured relative to carbon assimilation,

and sweetveld occurs. At high water availability, carbon assimilation continues, but nitrogen is lost by nitrification and leaching. Sourveld therefore occurs in wet areas. The optimum temperature for carbon assimilation is approximately 25°C, while that for nitrogen mineralization is approximately 40°C. At low temperatures, carbon assimilation is favoured relative to nitrogen mineralization, and sourveld occurs. At high temperatures, nitrogen mineralization is favoured, and sweetveld occurs.

Soil characteristics, including texture and fertility also affect the distribution of sweetveld and sourveld. Soils with a high clay content yield less water to plants in semi-arid situations than sandy soils, yet they have a higher water content below wilting point, in which soil microbes are able to function. These conditions favour nitrogen mineralization relative to carbon assimilation. At high rainfall, the effect of soil type on moisture conditions is overridden by rainfall itself. Soils with high inherent fertility, such as those derived from basic igneous rocks, support sweetveld in areas where the climate may favour the occ ence of sourveld. Conversely, soils with low fertility, such as those derived from quartzite or sandstone support sourveld irrespective of climate. This is related to the extent to which organically bound nitrogen is protected is these soils, being greater in soils with a high clay content, particularly where these have a large surface area, such as the smectite group.

The model developed in this study is supported by direct evidence, both in the distribution if these vegetation types as well as in the response of sourveld to experimental manipulations such as burning and mowing. It is also supported by indirect evidence, including the abundance of grasses with a high concentration of structural tissue such as the wiregrasses, as well as those with high levels of nitrogen free compounds such as tannins, in areas where carbon assimilation is favoured relative to nitrogen assimilation.

8.2 APPLYING THE MODELS: THE CONSEQUENCES OF A SCENARIO OF CLIMATE CHANGE FOR BIOME DISTRIBUTION

The use of predictive models in the form of decision trees, such as those presented in chapters 4 and 7 make results explicitly testable, and focus attention on shortcomings. They also enable prediction of the response of vegetation to climatic

and man-induced change. The use of one of these models in predicting the response of vegetation to a scenario of climate change is illustrated. The response of vegetation to a hypothetical 2°C increase in temperature and a 15% decrease in rainfall will be illustrated at the subcontinental scale. This scenario is simplified, but is one of several possible scenarios of climate change in the twenty-first century (Schneider 1992).

Given a 2°C increase in temperature and a 15% decrease in rainfall, the biome model predicts that in the long-term the grassland biome would be invaded by savanna on a relatively large scale, both east and west of the escarpment (Fig. 8.1). It also predicts an expansion of succulent karoo at the expense of fynbos in the south-western Cape, although the mountainous topography and microclimatic variation associated with this region makes detailed prediction difficult. The model further predicts an expansion of nama-karoo into the savannas of the northern Cape Province, and possibly into the grasslands of the western Orange Free State.

Modelling the response of vegetation to a scenario of climate change, as described above, is considered to have several advantages:

- it is relatively simple and robust, matching the scale and quality of the data that climate models are presently able to provide in predicting climatic change scenarios;
- it highlights the processes that need to be studied in detail;
- it indicates the geographic regions where long-term studies are most likely to detect climate-induced vegetation shifts; and
- it indicates the type of information that is needed from climate models to predict vegetation responses to climate change.

The disadvantages of using the present model are that it predicts only the direction and not the rate of change, and that it remains largely empirical rather than mechanistic. In this last respect, this model is a considerable improvement over other schemes which rely on climatic indices with no attempt at biological interpretation. It is however appropriate as an initial 'strategic' modelling step, the purpose of which is to identify geographical regions and ecological processes which require more detailed investigation.

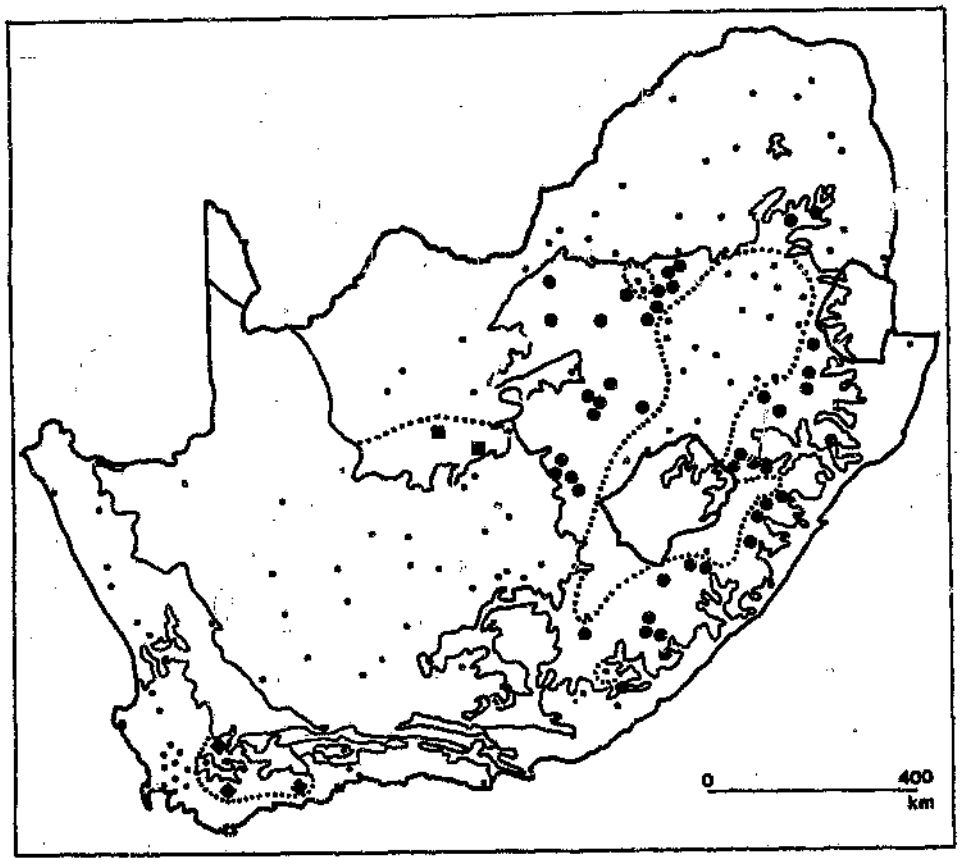


Figure 8.1: Changes in the distribution of South Africa's biomes based on a classification of weather stations assuming a 2° C increase in mean maximum and minimum monthly temperatures, and a 15% increase in rainfall. Solid lines indicate the present distribution of biomes (after Rutherford & Westfall 1986; cf. Fig. 4.1). Stations that were classified as belonging to the same biome as before this scenario of change are indicated as dots, those that changed status as large solid symbols (diamonds = succulent karoo, squares = nama-karoo, circles = savanna). Dotted lines represent the inferred distribution of biomes given this scenario of change. The most marked change in the distribution of biomes is the invasion of grassland by savanna.

8.3 FUTURE RESEARCH

8.3.1 THE DISTRIBUTION OF THE GRASSLAND BIOME

The distribution of the grassland biome in South Africa has been linked to climate and fire. Any environmental feature which promotes fire frequency or intensity, or which enables fire spread, would favour grassland over nama-karoo and forest. Savanna species are tolerant of fire. Their distribution is limited by low dry season temperatures, or by some correlate of this, such as frost. Future research aimed at clarifying the contribution of these factors to the distribution of grasslands should be by way of calibration and modelling.

A suitable approach would be to develop predictive models of grassland productivity in relation to the environment. These would provide a basis for predicting standing crop at some time after a fire. Fire frequency and intensity would need to be rated on the basis of standing crop, and on the occurrence of climatic conditions which desiccate vegetation and/or promote fire, such as berg winds, frosts or lightning. The effect of topography in relation to the prevailing winds during the fire prone season on fire frequency, intensity and spread also need to be investigated.

The effects of low temperatures on savanna species needs to be investigated to establish what aspects of the dry season temperature in the grassland biome affects the distribution of savanna trees. Alternatively, it may be that low temperatures at the beginning and end of the wet season in the grassland biome limit the growth of savanna trees, or it may be the absolute temperatures in the dry sason in the grassland biome that limit the growth of savanna trees. It may be a combination of factors. The effect of the presence of grasses on the growth of savanna trees given climatic constraints of the grassland biome also needs to be established. Is it through fire effects, or competition for resources?

8.3.2 THE DISTRIBUTION AND SEASONAL FORAGE QUALITY DYNAMICS OF SWEETVELD, MIXED VELD AND SOURVELD

The second aspect that warrants more detailed investigation is the question of the

distribution and forage quality dynamics of sweetveld, mixed veld and sourveld. A conceptual model has been proposed on the basis of the present spatial distribution of these three vegetation units. The model needs to be empirically tested. To do this, carbon assimilation and nitrogen mineralization should be measured in situ for several seasons, in a range of veld types, and covering a range of soil types and climatic conditions. Ideally, this should be integrated into the performance of organisms at the next trophic level, providing a quantitative basis for distinguishing sweetveld, mixed veld and sourveld. Experimental procedures could be used to calibrate different components, such as the effect of different soil types on carbon and nitrogen metabolism, and the effect of different management regimes on forage quality dynamics.

To develop mechanistic understanding, the model should also be calibrated, so that the balance between carbon and nitrogen assimilation that determines whether veld is sweet, mixed or sour can be determined. A pertinent question is "what is the ratio of carbon to nitrogen that maintains animal performance?" The effects of manipulations on this balance need to be quantified in order to improve management to maximise yield, particularly of the herbivore component.

REFERENCES

ACOCKS J.P.H. 1953. Veld types of South Africa. Mem. Bot. Surv. S. Afr. No. 28.

ACOCKS J.P.H. 1964. Karoo vegetation in relation to the development of deserts. In: D.H.S. Davis ed. Ecological studies in southern Africa. Junk, The Hague. pp. 100-112.

ACOCKS J.P.H. 1975. Veld types of South Africa. Mem. Bot. Surv. S. Afr. No. 40.

ACOCKS J.P.H. 1988. Veld types of South Africa. Mem. Bot. Surv. S. Afr. No. 57.

ADAMSON R.S. 1938. The vegetation of South Africa. British Empire Vegetation Committee, London.

ALBERTI L. 1807. Account of the tribal life and customs of the Xhosa in 1807. Translated by Fehr 1968. AA Balkema, Cape Town.

AMER F., BOULDIN D.R., BLACK, C.A. & DUKE F.R. 1955. Characterization of soil phosphorus by anion exchange resin adsorption and ^{32}P equilibration. Plant Soil 6:391-408.

ANDERSON R.C. 1982. An evolutionary model summarising roles of fire, climate and grazing animals in the origin and maintenance of grasslands: an end paper. In: J.R. Estes, R.J. Tyrl & J.N. Bunken eds. Grasses and grasslands: systematics and evolution. Oklahoma University Press, Norman, Oklahoma. pp. 297-308.

ANDERSON J.M. & INGRAM J.S.I. 1989. Tropical soil biology and fertility: A handbook of methods. CAB International, Wallingford.

ARMSTRONG W. 1975. Waterlogged soils. In: J.R. Etherington ed. Environment and plant ecology. John Wiley & Sons, London. pp. 181-218.

ARRIS L.L. & EAGLESON P.S. 1989. Evidence of a physiological basis for the boreal-deciduous forest ecotone in North America. Vegetatio 82:55-58.

AUCKAMP A.J., DANCKWERTS J.E., TEAGUE W.R. & VENTER J.J. 1983. The role of *Acacia karroo* in the false thornveld of the eastern Cape. Proc. Grassld. Soc. Sth. Afr. 18:151-154.

AXELROD D.I. 1985. The rise of the grassland biome, central North America. Bot. Rev. 51:163-201.

AYOADE J.O. 1988. Tropical hydrology and water resources. Macmillan Publishers, London.

BARKMAN J.J. 1988. New systems of plant growth forms and phenological plant types. In: M.J.A. Werger, P.J.M. van der Aart, H.J. During & J.T.A Verhoeven eds. Plant form and vegetation structure. SPB Academic Publishing, The Hague. pp. 9-44.

BAYER A.W. 1955. The ecology of grasslands. In: D. Meredith ed. The grasses and pastures of South Africa. CNA Ltd., Parow. pp. 539-550.

BAZZAZ F.A., CHIARIELLO N.R., COLEY P.D. & PITELKA L.F. 1987. Allocating resources to reproduction and defense. BioScience 37:58-67.

BEARD J.S. 1978. The physiognomic approach. In: R.H. Whittaker ed. Classification of plant communities. Junk, The Hague. pp. 33-64.

BEWS J.W. 1918. The grasses and grasslands of South Africa. Davies & Sons, Pietermaritzburg.

BEWS J.W. 1929. The worlds grasses: Their differentiation, distribution, economics and ecology. Longmans, Green & Co., London.

BOND W.J. & RICHARDSON D.M. 1990. What can we learn from extinctions and invasions about the effects of climate change? S. Afr. J. Sci. 86:429-433.

BOOYSEN P. de V. 1981. The establishment of cultivated pastures. In: N.M. Tainton ed. Veld and pasture management in South Africa. Shuter and Shooter, Pietermaritzburg. pp. 91-117.

BORCHERT J.R. 1950. The climate of the central North American grassland. Ann. Assoc. Amer. Geogr. 40:1-39.

BOUTTON T.W., HARRISON A.T. & SMITH B.N. 1980. Distribution of biomass of species differing in photosynthetic pathway along an altitudinal transect in southeastern Wyoming grassland. Oecologia 45:287-298.

BOX E.O. 1981a. Macroclimate and plant forms: an introduction to predictive modelling in phytogeography. Junk, The Hague.

BOX E.O. 1981b. Predicting physiognomic vegetation types with climatic variables. Vegetatio 45:127-139.

BRAIN C.K. & SILLEN A. 1988. Evidence from the Swartkrans cave for the earliest use of fire. Nature 336:464-466.

BRANSBY D.I. 1981. Forage quality. In: N.M. Tainton ed. Veld and pasture management in South Africa. Shuter & Shooter, Pietermaritzburg. pp. 57-90.

BRAUN-BLANQUET J. 1965. Plant sociology: The study of plant communities. Translated by G.D. Fuller & H.S. Conard. Hafner, London.

BRYANT J.P., CHAPIN F.S. III, & KLEIN D.R. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40:357-368.

BRYANT J.P. & KUROPAT P.J. 1980. Selection of winter forage by subarctic browsing browsing vertebrates: The role of plant chemistry. Ann. Rev. Ecol. Syst. 11:261-285.

BRYANT J.P., REICHARDT P.B. & CLAUSEN T.P. 1992. Chemically mediated interactions between woody plants and browsing mammals. J. Range Manage. 45:18-24.

BUDYKO M.I. 1974. Climate and life. Academic Press, New York.

CABLE J.C.H., SCOTT K. & CARTER P.L. 1980. Excavations at Good Hope shelter, Underberg district, Natal. Annals of the Natal Museum, 24:1-34.

CAIN S.A. 1950. Life forms and phytoclimates. Bot. Rev. 16:1-32.

CARTER P.L. 1970. Late Stone Age exploitation patterns in southern Natal. S. Afr. Archaeol. Bull. 25:55-59.

CATALDO,D.A., HAROON M., SCHRADER L.E. & YOUNGS V.L. 1975. Rapid colorimetric determination of nitrate in plant tissue by nitration of salicylic acid. Communications in Soil Science and Plant Nutrition 6:71-80.

CAVAGNARO J.B. 1988. Distribution of C_3 and C_4 grasses at different altitudes in a temperate arid region of Argentina. Oecologia 76:273-277.

CHAPIN F.S. III. 1980. The mineral nutrition of wild plants. Ann. Rev. Ecol. Syst. 11:233-260

CHAPIN F.S. III, BLOOM A.J., FIELD C.B. & WARING R.H. 1987. Plant responses to multiple environmental factors. BioScience 37:49-57.

CHAPIN F.S. III, VITOUSEK P.M. & VAN CLEVE K. 1986. The nature of nutrient limitation in plant communities. Am. Nat. 127:48-58.

CHAPMAN J.D. & WHITE F. 1970. The evergreen forests of Malawi. Commonwealth Forestry Institute, Oxford.

CHRISTENSEN N.L. 1977. Fire and soil-plant nutrient relations in a pine wiregrass savanna on the coastal plain of North Carolina. Oecologia 31:27-44

CHRISTENSEN N.L. 1987. The biogeochemical consequences of fire and their effects on the vegetation of the coastal plain of the southeastern United States. In: L. Trabaud ed. The role of fire in ecological systems. SPB Academic Publishing, The Hague. pp. 1-21.

CLARK J.S. 1988. Effect of climate change on fire regimes in northwestern Minnesota. Nature 334:233-235.

CLARK J.S. 1989. Effects of long-term water balances on fire regime, north-western Minnesota. J. Ecol. 77:989-1004.

COATES-PALGRAVE K. 1977. Trees of southern Africa. C. Struik Publishers, Cape Town.

COCK E. & KOCH J. 1991. Going green. People, politics and the environment in South Africa. Oxford University Press, Cape Town.

COLEMAN D.C., REID C.P.P. & COLE C.V. (1983) Biological strategies of nutrient cycling in soil systems. Adv. Ecol. Res. 13:1-55.

COLEY P.D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. Ecol. Monogr. 53:209-233.

COLEY P.D., BRYANT J.P. & CHAPIN F.S. III. 1985. Resource availability and plant antiherbivore defense. Science 230:895-899.

COLLINS R.F. & JONES M.B. 1985. The influence of climatic factors on the distribution of C_4 species in Europe. Vegetatio 64:121-129.

COOPER C.F. 1961. The ecology of fire. Sci. Amer. 204:150-160.

COUTEAUX M.-M., MOUSSEAU M., CELERIER M.-L. & BOTTNER P. 1991. Increased atmospheric CO_2 and litter quality: decomposition of sweet chestnut leaf litter with animal food webs of different complexities. Oikos 61:54-64.

COWLING R.M. 1983. The occurrence of C_3 and C_4 grasses in fynbos and allied shrublands in the south eastern Cape, South Africa. Oecologia 58:121-127.

COX T.F. 1976. The robust estimation of the density of a forest stand using a new conditioned distance method. Biometrika 63:493-499.

DEBELL D.S. & RALSTON C.W. 1970. Release of nitrogen by burning light forest fuels. Soil Sci. Soc. Amer. Proc. 34:936-938.

DICKINSON C.H. 1974. Decomposition of plant litter in soil. In: C.H. Dickinson & G.J.F. Pugh eds. Biology of plant litter decomposition. Academic Press, London. pp. 633-658.

DIMBLEBY G.W. 1977. Ecology and Archaeology Studies in Biology No. 77, Edward Arnold, London.

DORICH R.A. & NELSON D.W. 1983. Direct colorimetric measurement of ammonium in potassium chloride extracts in soil. Soil Sci. Soc. Am. J. 47:833-836.

DOWNING B.H., ROBINSON E.R., TROLLOPE W.S.W. & MORRIS J.W. 1978. Influence of macchia eradication techniques on botanical composition of grasses in the Dohne sourveld of the Amatole mountains. Proc. Grassld. Soc. Sth. Afr. 13:111-115.

DU TOIT E.W., WOLFSON M.M. & ELLIS R.P. 1991. The presence of condensed tannin in the leaves of *Eulalia villosa*. J. Grassl. Soc. South. Afr. 8:74-76.

DU TOIT P.F. 1972. *Acacia karoo* intrusion: The effect of burning and sparing. Proc. Grassld. Soc. Sth. Afr. 7:23-27.

EDWARDS D. 1983. A broad-scale structural classification of vegetation for practical purposes. Bothalia 14:705-712.

EDWARDS D. 1984. Fire regimes in the biomes of South Africa. In: P. de V. Booysen & N.M. Tainton eds. Ecological effects of fire in South African ecosystems. Springer Verlag, Berlin. pp. 19-37.

ELLERY K., ELLERY W.N. & VERHAGEN B.Th. 1992. The distribution of C_3 and C_4 plants in a successional sequence in the Okavango delta. S. Afr. J. Bot. 58:400-402.

ELLERY W.N. & MENTIS M.T. In press. How old are South Africa's grasslands? Accepted for publication in the conference proceedings on forest - savanna boundaries. Glasgow 1990.

ELLERY, W.N., MENTIS, M.T. & SCHOLES, R.J. In press. Modelling the location of woody-grassland boundaries. Accepted for publication in the conference proceedings on forest - savanna boundaries. Glasgow 1990.

ELLERY, W.N., SCHOLES, R.J. & MENTIS, M.T. 1991. Differentiation of the grassland biome of South Africa based on climatic indices. S. Afr. J. Sci. 87:499-503.

ELLIS R.P. 1977. Distribution of the Kranz syndrome in the southern African Eragrostoideae and Panicoideae according to bundle sheath anatomy and cytology. Agroplantae 9:73-110.

ELLIS R.P. 1990. Tannin-like substances in grass leaves. Mem. Bot. Surv. S. Afr. No. 59.

ELLIS R.P., VOGEL J.C. & FULS A. 1980. Photosynthetic pathways and the geographical distribution of grasses in South West Africa/Namibia. S. Afr. J. Sci. 76:307-314.

EVERSON T.M., VAN WILGEN, B.W. & EVERSON C.S. 1988. Adaptation of a model for rating fire danger in the Natal Drakensberg. S. Afr. J Sci. 84:44-49.

FEELY J.M. 1980. Did Iron Age man have a role in the history of Zululand's wilderness landscapes? S. Afr. J. Sci. 76:150-152.

FEELY J.M. 1987. The early Farmers of Transkei, Southern Africa. Cambridge Monographs in African Archaeology No. 24.

FITZPATRICK E.A. & NIX H.A. 1970. The climatic factor in Australian grasslands. In: R.M. Moore ed. Australian Grasslands. Australian National University Press, Canberra. pp. 3-26.

FRIEDEL M.H. 1987. A preliminary investigation of woody plant increase in the western Transvaal and implications for veld assessment. J. Grassld. Soc. South. Afr. 4:25-30.

FROST P.G.H, MENAUT J-C., WALKER B.H., MEDINA E., SOLBRIG O.T. & SWIFT M.J. 1986. Responses of savannas to stress and disturbance. A proposal for a collaborative programme of research. Report of an IUBS working group on Decade of the Tropics Programme/Tropical savanna ecosystems, Harare, Zimbabwe.

GARNIER B.J. & OHMURA A. 1968. A method of calculating the direct shortwave radiation income of slopes. J. Appl. Meteorol. 7:796-800.

GIBBS RUSSEL G.E. 1987. Preliminary floristic analysis of the major biomes in southern Africa. Bothalia 17:213-227.

GIBBS RUSSELL G.E., WATSON L., KOEKEMOER M., SMOOK L., BARKER N.P., ANDERSON H.M. & DALLWITZ M.J. 1990. Grasses of southern Africa. Mem. Bot. Surv. S. Afr. No. 58.

GIBBS RUSSELL G.E., WELMAN W.G., RETIEF E., IMMELMAN K.L., GERMISHUIZEN G., PIENAAR B.J., VAN WYK M. & NICHOLAS A. 1987. List of species of Southern African Plants. Edition 2, Part 2. Mem. Bot. Surv. S. Afr. No. 56.

GLOVER P.E., GLOVER J. & GWYNNE M.D. 1962. Light rainfall and plant survival in east Africa. II Dry grassland vegetation. J. Ecol. 50:199-206.

GOODESS C.M. & PALUTIKOF J.P. 1992. The development of regional climate scenarios and the ecological impact of greenhouse gas warming. Adv. Ecol. Res. 22:33-62.

GRANGER 1984. Fire in forest. In: P. de V. Booysen & N.M. Tainton eds. Ecological effects of fire in South African ecosystems. Springer Verlag, Berlin.

GRIFFIN D.M. 1972. Ecology of soil fungi. Chapman & Hall, London.

GRIME J.P. 1974. Vegetation classification by reference to strategies. Nature 250:26-31.

GRIME J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111:1169-1194.

GRIME J.P. 1985. Towards a functional description of vegetation. In: J. White ed. The population structure of vegetation. Junk Publishers, Dordrecht.

HALL M. 1984. Man's historical and traditional use of fire in southern Africa. In: P. de V. Booysen & N.M. Tainton eds. Ecological effects of fire in South African ecosystems. Springer Verlag, Berlin. pp. 39-52.

HALL M. 1987. The Changing Past: Farmers, Kings and Traders in Southern Africa, 200-1860. David Phillip, Cape Town.

HALL M. & MAGGS T. 1979. Nqabeni, a Late Iron Age site in Zululand. South African Archaeological Society Goodwin Series, 3:159-175.

HALL S.L. 1986. Pastoral adaptations and forager reactions in the eastern Cape. South African Archaeological Society Goodwin Series, 5:42-49.

HARMSE H.J. 1978. Schematic soil map of southern Africa south of latitude 16°30'S. In: M.J.A. Werger ed. Biogeography and ecology of southern Africa. Junk, The Hague.

HATCH M.D. & SLACK C.R. 1966. Photosynthesis by sugar-cane leaves. Biochem. J. 101:103-111.

HATTERSLEY P.W. 1983. The distribution of C_3 and C_4 grasses in Australia in relation to climate. Oecologia 57:113-128

HILL M.O. 1979. TWINSPAN - A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Ithaca, New York.

HOFFMAN T.M. & COWLING, R.M. 1990. Vegetation change in the semi-arid eastern karoo over the last 200 years: an expanding karoo: Fact or fiction? S. Afr. J. Sci. 86:286-294.

HOLDRIDGE L.R. 1967. Life zone ecology. Revised edition. Tropical Science Center, San Jose, Costa Rica.

HULBERT L.C. 1988. Causes of fire effects in tallgrass prairie. Ecology 69:46-58.

HUNTLEY B.J. 1984. Characteristics of South African Biomes. In: P. de V. Booysen & N.M. Tainton eds. Ecological effects of fire in South African ecosystems. Springer Verlag, Berlin.

HUNTLEY B.J. 1989. Biotic diversity in southern Africa: Concepts and conservation. Oxford University Press, Cape Town.

HUNTLEY, B.J., SIEGFRIED, W.R. & SUNTER, C. 1989. South African Environments Into the 21st Century. Human & Rouseau, Cape Town.

JACKSON S.P. 1952. Atmospheric circulation over South Africa. S. Afr. Geogr. J. 34:48-60.

JOHNSON R.W. & TOTHILL J.C. 1985. Definitions and broad geographic outline of savanna lands. In: J.C. Tothill & J.J. Mott eds. Ecology and management of the world's savannas. Australian Academy of Science, Canberra. pp. 1-13.

JORDAAN J. 1991. Population growth - our time bomb. J.L. van Schaik, Pretoria.

KEENEY D.R. 1982. Nitrogen-availability indices. In: A.L. Page, R.H. Miller & D.R. Keeney eds. Methods of soil analysis. Part 2. American Society of Agronomy, Wisconson.

KILLICK D.J.B. 1963. An account of the plant ecology of the Cathedral Peak area of the Natal Drakensberg. Mem. Bot. Surv. S. Afr. No. 34.

KILLICK D.J.B. 1978. The Afro-alpine region. In: M.J.A. Werger ed. Biogeography and ecology of southern Africa. Junk, The Hague. pp. 515-560.

KING L.C. 1978. The geomorphology of central and southern Africa. In: M.J.A. Werger ed. Biogeography and ecology of southern Africa. Junk, The Hague. pp. 1-19.

KING L.C. 1982. The Natal monocline: Explaining the origin and scenery of Natal, South Africa. 2nd Ed. University of Natal Press, Pietermaritzburg.

KIRKMAN K.P. 1988. Factors affecting the seasonal variation of veld quality in South Africa. MSc (Agric.) thesis, University of Natal, Pietermaritzburg.

KLEIN R.G. 1984. The large mammals of southern Africa: Late Pliocene to recent. In: R.G. Klein ed. Southern African prehistory and palaeoenvironments. Balkema, Rotterdam. pp. 107-146.

KORTSCHACK H.P., HART C.E. & BURR G.O. 1965. Carbon dioxide fixation in sugarcane leaves. Plant Physiol. 40:209-213.

KRIGE E.J. 1936. The social system of the Zulus. Shuter & Shooter, Pietermaritzburg.

KRUGER F.J. 1979. Fire. In: J. Day, W.R. Siegfried, G.N. Louw & M.L. Jarman eds. Fynbos ecology: a preliminary synthesis. South African National Scientific Programmes Report No. 40.

KRUGER F.J. & BIGALKE R.C. 1984. Fire in fynbos. In: P. de V. Booysen & N.M. Tainton. eds. Ecological effects of fire in South African ecosystems. Springer Verlag, Berlin.

LANGER R.H.M. 1972. How grasses grow. Edward Arnold, London.

LINACRE E.T. 1977. A simple formula for estimating evaporation rates in various climates, using temperature data alone. Agric. Meteorol. 18:409-424.

MACARTHUR R.H. & WILSON E.O. 1967. The theory of island biogeography. Princeton University Press, Princeton.

MACDUFF J.H. & WHITE R.E. 1985. Net mineralization and nitrification rates in a clay soil measured and predicted in permanent grassland from soil temperature and moisture content. Plant and Soil 86:151-172.

MACVICAR C.N., LOXTON R.F., LAMBRECHTS J.J.N, LE ROUX J., DE VILLIERS J.M., VERSTER E., MERRYWEATHER F.R., VAN ROOYEN T.H. & HARMSE J.J. VON M. 1977. Soil classification: A binomial system for South Africa. Department of Agricultural and Technical Services, Pretoria.

MAGGS T. 1976. Iron Age communities of the southern Highveld. Natal Museum Occasional Paper No. 2.

MAGGS T. 1984. The Iron Age south of the Zambezi. R.G. Klein ed. Southern African prehistory and palaeoenvironments. Balkema, Rotterdam. pp. 329-360.

MAGGS T. & WARD V. 1980. Driel Shelter: Rescue at a late Stone Age site on the Tugela River. Annals of the Natal Museum, 24:35-70.

MANRY D.E. 1982. Habitat use by foraging bald ibises *Geronticus calvus* in western Natal. S. Afr. J. Wildl. Res. 12:85-93.

MANRY D.E. & KNIGHT R.S. 1986. Lightning density and burning frequency in South African vegetation. Vegetatio 66:67-76.

MATHER J.R. & YOSHIOKA G.A. 1968. The role of climate in the distribution of vegetation. Ann. Assoc. Am. Geogr. 58:29-41.

MATTSON W.J. 1980. Herbivory in relation to plant nitrogen content. Ann. Rev. Ecol. Syst. 11:119-161.

MCNAUGHTON, S.J., COUGHENOUR M.B. & WALLACE L.L 1982. Interactive processes in grassland ecosystems. In: J.R. Estes, R.J. Tyrl & J.N. Bunken eds. Grasses and grasslands: systematics and evolution. Oklahoma University Press, Norman, Oklahoma. pp. 167-193.

MEADOWS M.E. 1983. Past and present environments of the Nyika Plateau, Malawi. Palaeoecology of Africa, 16:353-390.

MEADOWS M.E. & MEADOWS K.F. 1988. Late Quarternary vegetation history of the Winterberg mountains, eastern Cape, South Africa. S. Afr. J. Sci. 84:253-259.

MEETENMEYER V. 1978. Macroclimate and lignin control of litter decomposition rates. Ecology 59:465-472

MEISSNER H.H. 1983. Effects of energy concentration and feeding level on growth and efficiency of beef steers. S. Afr. J. Anim. Sci. 13:80-83.

MENTIS M.T., MEIKLEJOHN M.J. & SCOTCHER J.S.B. 1974. Veld burning in Giants Castle Game Reserve, Natal Drakensberg. Proc. Grassld. Soc. Sth. Afr. 9:26-31.

MENTIS M.T. & BIGALKE R.C. 1979. Some effects of fire on two grassland francolins in the Natal Drakensberg. S. Afr. J. Wildl. Res. 9:1-8.

MENTIS M.T. & HUNTLEY B.J. 1982. A description of the Grassland Biome Project. South African National Scientific Programmes Report No. 62.

MENTIS M.T. & ROWE-ROWE D.T. 1979. Fire and faunal abundance and diversity in the Natal Drakensberg. Proc. Grassld. Soc. Sth. Afr. 14:75-77.

MES M.G. 1958. The influence of veld burning or mowing on the water, nitrogen and ash content of grasses. S. Afr. J. Sci. 54:83-86.

MOON B.P. & DARDIS G.F. 1988. Introduction. In: B.P. Moon & G.F. Dardis eds. The geomorphology of southern Africa. Southern Book Publishers, Johannesburg. pp. 1-11.

MORREY D.R., BALKWILL K. & BALKWILL M.-J. 1989. Studies on serpentine flora: Preliminary analyses of soils and vegetation associated with serpentine rock formations in the south-eastern Transvaal. S. Afr. J. Bot. 55:171-177.

MURPHY J. & RILEY J.P. 1962. A modified single solution method for the determination of phosphate in natural waters. Analytica Chemica Acta 27:31-36.

NELSON D.W. & SOMMERS L.E. 1975. A rapid and accurate procedure for estimation of organic carbon in soils. Proc. Indiana Acad. Sci. 84:456-462.

NOBLE I.R. & SLATYER R.O. 1979. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43:5-21.

O'CONNOR T.G. 1991. Local extinction in perennial grasslands: A life history approach. Am. Nat. 137:753-773.

OLLIER C.D. & MARKER M.E. 1985. The Great Escarpment of southern Africa. Zeitschrift fur Geomorphologie Supp. 54:37-56.

OWEN-SMITH N. & NOVELLIE P. 1982. What should a clever kudu eat? Am. Nat. 119:151-178.

PARTRIDGE T.C. & MAUD R.R. 1987. Geomorphic evolution of southern Africa since the Mesozoic. S. Afr. J. Geol. 90:179-208.

PEARCY R.W. & EHLERINGER J. 1984. Comparative ecophysiology of C_3 and C_4 plants. Plant Cell Environ. 7:1-13.

PHILLIPS E.P. 1919. A preliminary report on the veld burning experiments at Groenkloof, Pretoria. S. Afr. J. Sci. 16:286-299.

PHILLIPS J.F.V. 1930. Fire: Its influence on biotic communities and physical factors in South and East Africa. S. Afr. J. Sci. 27:352-367.

PHILLIPS J.F.V. 1971. Physiognomic classification of the more common vegetation types in South Africa, including Mocambique. Loxton Hunting & Associates, Johannesburg.

POLE EVANS I.B. 1920. The veld: Its resources and dangers. S. Afr. J. Sci. 17:1-34.

POLE EVANS I.B. 1936. A vegetation map of South Africa. Mem. Bot. Surv. S. Afr. No. 15.

PRATT D.J. & GWYNNE M.D. 1977. Rangeland management and ecology in east Africa. Hodder & Stoughton, London.

PURCHASE B.S. 1974. The influence of phosphate deficiency on nitrification. Plant Soil 41:541-547.

RAISON R.J. 1979. Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations: a review. Plant Soil 51:73-108.

RAUNKAIER C. 1934. The life forms of plants and statistical plant geography. Oxford University Press, Oxford.

ROBERTS B.R. 1973. Common grasses of the Orange Free State. OFS Prov. Admin. Nature Conserv. Misc. Publ. No. 3.

RODGERS C.S. & ANDERSON R.C. 1979. Presettlement vegetation of two prairie peninsula counties. Bot. Gaz. 140:232-240.

ROSENZWEIG L.M. 1968. Net primary productivity of terrestrial communities: prediction from climatological data. Am. Nat. 102:67-74.

ROUX P.W. & THERON G.K. 1987. Vegetation change in the karoo biome. In: R.M. Cowling & P.W. Roux eds. The karoo biome: A preliminary synthesis. Part 2. Vegetation history. South African National Scientific Programmes Report No. 142. pp. 50-69.

ROUX P.W. & VORSTER M. 1983. Vegetation change in the Karoo. Proc. Grassld. Soc. Sth. Afr. 18:25-29.

RUNDEL P.W. 1980. The ecological distribution of C_3 and C_4 grasses in the Hawaiian islands. Oecologia 45:354-359.

RUNNING S.W., NEMANI R.R. & HUNGERFORD R.D. 1987. Extrapolation of synoptic meteorological data in mountainous terrain and its use for simulating forest evapotranspiration and photosynthesis. Can. J. For. Res. 17:472-483.

RUTHERFORD M.C. 1978. Primary production ecology in southern Africa. In: M.J.A. Werger ed. Biogeography and ecology of southern Africa. Junk, The Hague.

RUTHERFORD M.C. 1980. Annual plant production-precipitation relations in arid and semi-arid regions. S. Afr. J. Sci. 76:53-56.

RUTHERFORD M.C. & WESTFALL R.H. 1986. Biomes of southern Africa - an objective categorization. Mem. Bot. Surv. S. Afr. No. 54.

SABEY B.R. & JOHNSON D.D. 1971. Effect of soil moisture tension on nitrate accumulation in Drummer silty clay loam. Soil Sci. Soc. Amer. Proc. 35:848-850.

SAS. 1985. SAS user's guide: statistics. Version 5. SAS Institute, Cary, North Carolina.

SAVAGE M.J. 1980. The effect of fire on the grassland microclimate. Herbage Abstracts 50:589-603.

SCHLESINGER W.H. 1989. The role of ecologists in the face of global change. Ecology 70:1.

SCHNEIDER S.H. 1992. The climatic response to greenhouse gases. Adv. Ecol. Res. 22:1-32.

SCHULZE E.-D. 1986. Carbon dioxide and water vapour exchange in response to drought in the atmosphere and in the soil. Ann. Rev. Plant Physiol. 37:247-274.

SCHULZE R.E. & MCGEE O.S. 1978. Climatic indices and classifications in relation to the biogeography of southern Africa. In: M.J.A. Werger ed. Biogeography and ecology of southern Africa. Junk, The Hague. pp. 19-52.

SCOTT J.D. 1947. Veld management in South Africa. Bulletin 278, Government Printer, Pretoria.

SHACKLETON C.M. 1989. The grassland dynamics of Mkambati game reserve. MSc thesis, University of the Witwatersrand, Johannesburg.

SHACKLETON L. 1990. Studies of global change in southern Africa. S. Afr. J. Sci. 86:278.

SIBBENSEN E. 1978. An investigation of the anion exchange resin method for soil phosphate extraction. Plant Soil 50:305-321.

SIEGFRIED W.R. 1971. The status of the bald ibis of southern Africa. Biological Conservation 3:88-91.

SIEGFRIED W.R. 1989. Preservation of species in southern African nature reserves. In: B.J. Huntley ed. Biotic diversity in southern Africa. Oxford University Press, Cape Town. pp. 186-201.

SIMBERLOFF D. & DAYAN T. 1991. The guild concept and the structure of ecological communities. Ann. Rev. Ecol. Syst. 22:115-143.

SIMS P.L. 1988. Grasslands. In: M.G. Barbour & W.D. Billings eds. North American terrestrial vegetation. Cambridge University Press, Cambridge. pp. 265-286.

SINCLAIR A.R.E. 1974. The natural regulation of buffalo populations in East Africa. IV. The food supply as a regulating factor, and competition. E. Afr. Wildl. J. 12:291-311.

SINCLAIR A.R.E. 1975. The resource limitation of trophic levels in tropical grassland ecosystems. J. Animal Ecol. 44:497-520.

SINGH J.S. & GUPTA S.R. 1977. Plant decomposition and soil respiration in terrestrial ecosystems. Bot. Rev. 43:449-528.

SMITH S.J., YOUNG L.B. & MILLER G.E. 1977. Evaluation of soil nitrogen mineralization potentials under modified field conditions. Soil Sci. Soc. Am. J. 41:74-76.

SMITH T.M., SHUGART H.H., BONAN G.B. & SMITH J.B. 1992. Modeling the potential response of vegetation to global climate change. Adv. Ecol. Res. 22:93-116.

SOGA J.M. 1930. The south-eastern Bantu. Bantu Studies No. 4. Witwatersrand University Press, Johannesburg.

SOIL SURVEY STAFF 1960. Soil classification - a comprehensive system (7th approximation). US Department of Agriculture, Washington.

SOWELL J.B. 1985. A Predictive model relating North American plant fromations and climate. Vegetatio 60:103-111.

SPECHT R.L. 1981. Growth indices - their role in understanding the growth, structure and distribution of Australian vegetation. Oecologia 50:347-356.

STALMANS M.E. 1990. Vegetation survey for the scientific management of the Lekgalameetse Nature Reserve. MSc Thesis, University of the Witwatersrand, Johannesburg, South Africa.

STANFORD G. & EPSTEIN E. 1974. Nitrogen mineralization - water relations in soils. Soil Sci. Soc. Amer. Proc. 38:103-106.

STANFORD G., FRERE M.H. & SCHWANINGER D.H. 1973. Temperature coefficient of soil nitrogen mineralization. Soil Science 115:321-323.

STANFORD G. & SMITH S.J. 1972. Nitrogen mineralization potentials of soils. Soil Sci. Soc. Amer. Proc. 36:465-472.

STEBBINS G.L. 1974. Flowering plants: Evolution above the species level. Edward Arnold, London.

STEPHENSON N.L. 1990. Climatic control of vegetation distribution: The role of the water balance. Am. Nat. 135:649-670.

STOCK W.D. & LEWIS O.A.M. 1986. Soil nitrogen and the role of fire as a mineralizing agent in a South African coastal fynbos ecosystem. J. Ecol. 74:317-328.

STOW G.W. 1905. The native races of South Africa. Swan Sonnenschein, London.

STUART-HILL G.C. & MENTIS M.T. 1982. Coevolution of African grasses and large herbivores. Proc. Grassld. Soc. Sth. Afr. 17:122-128.

SUNTER, C. 1987. The World and South Africa in the 1990s. Human & Rouseau, Cape Town.

TAINTON N.M. BRANSBY D.I. & BOOYSEN P. de V. 1976. Common veld and pasture grasses of Natal. Shuter & Shooter, Pietermaritzburg.

TAINTON N.M. 1981. Veld and pasture management in South Africa. Shuter & Shooter, Pietermaritzburg.

TAINTON N.M. 1984. A guide to the literature on research in the grassland biome of South Africa. South African National Scientific Programmes Report No. 96.

TAINTON N.M. & MENTIS M.T. 1984. Fire in grassland. In: P. de V. Booysen & N.M. Tainton eds. Ecological effects of fire in South African ecosystems. Springer-Verlag, Berlin. pp. 115-147.

TAINTON N.M., ZACHARIAS P.J.K. & HARDY M.B. 1989. The contribution of veld diversity to the agricultural economy. In: B.J. Huntley ed. Biotic diversity in southern Africa: Concepts and conservation. Oxford University Press, Cape Town.

TANKARD A.J., JACKSON M.P.A., ERIKSSON K.A., HOBDAY D.K., HUNTER, D.R. & MINTER W.E.L. 1982. Crustal evolution of southern Africa: 3.8 billion years of earth history. Springer-Verlag, New York.

TEERI J.A., STOWE L.G. & LIVINGSTONE D.A. 1980. The distribution of C_4 species of the Cyperaceae in North America in relation to climate. Oecologia 47:307-310.

TER BRAAK C.J.F. 1987. CANOCO - a FORTRAN program for canonical community ordination by (partial) (detrended) (canonical) correspondence analysis and redundancy analysis (version 2.1). ITI-TNO, Wageningen.

THORNTHWAITE C.W. 1948. An approach towards a rational classification of climate. Geogr. Rev. 38:55-94.

THORNTHWAITE C.W. 1952. Grassland climates. Proceedings of the Sixth International Grassland Congress, Pennsylvania State College.

TIESZEN L.L., SENYIMBA M.M., IMBAMBA S.K. & TROUGHTON J.H. 1979. The distribution of C_3 and C_4 grasses and carbon isotope discrimination along an altitudinal and moisture gradient in Kenya. Oecologia 37 337-350.

TINLEY, K.L. 1982. The influence of soil moisture balance on ecosystem patterns in southern Africa. In: B.J. Huntley & B.H. Walker eds. Ecology of tropical savannas. Springer Verlag, Berlin. pp. 175-192.

TROLLOPE W.S.W. 1973. Fire as a method of controlling macchia (fynbos) vegetation in the Amatole mountains of the eastern Cape. Proc. Grassl. Soc. Sth. Afr. 8:35-41.

TROLLOPE W.S.W. 1974. Role of fire in preventing bush encroachment in the eastern Cape. Proc. Grassl. Soc. Sth. Afr. 9:67-71.

TRUSWELL J.F. 1977. The geological evolution of South Africa. Purnell, Cape Town.

TYSON P.D. 1969. Atmospheric circulation and precipitation over South Africa. Environmental Studies Occasional Paper No. 2. Department of Geography and Environmental Studies, University of the Witwatersrand.

TYSON P.D. 1987. Climatic change and variability in southern Africa. Oxford University Press, Cape Town.

VAN DAALEN J.C. & GELDENHUYS C.J. 1988. Southern African forests. In: I.A.W. Macdonald & R.J.M. Crawford eds. Long-term data series relating to southern Africa's renewable natural resources. South African National Scientific Programmes Report No. 157. pp. 237-249.

VAN OUDTSHOORN F.P. 1991. Guide to grasses of South Africa. Briza Publications, Pretoria.

VAN VALEN L. 1971. Group selection and the evolution of dispersal. Evolution 25:591-598.

VOGEL, J.C., FULS, A. & ELLIS, R.P. 1978. The geographical distribution of Kranz grasses in South Africa. S. Afr. J. Sci. 74:209-215.

VOGEL J.C., FULS A. & DANNIN A. 1986. Geographical and environmental distribution of C_3 and C_4 grasses in the Sinai, Negev, and Judean deserts. Oecologia 70:258-265.

VOGL R. 1974. Effects of fire on grasslands. In: T.T. Kozlowski & C.E. Ahlgren eds. Fire and ecosystems. Academic Press, New York. pp. 139-194.

WALKER B.H., LUDWIG D., HOLLING C.S. & PETERMAN R.M. 1981. Stability of semi-arid savanna grazing systems. J. Ecol. 69:403-416.

WALKER B.H. & NOY-MEIR I. 1982. Aspects of stability and resilience of savanna ecosystems. In: B.J. Huntley & B.H. Walker eds. Ecology of tropical savannas. Springer Verlag, Berlin. pp. 556-590.

WALTER H. 1971. Ecology of tropical and subtropical vegetation. Translated by D. Mueller-Dombois. Oliver & Boyd, Edinburgh.

WEATHER BUREAU 1988. Climate of South Africa: Climate statistics up to 1984. 2nd edition. Weather Bureau, Department of Environment Affairs.

WEAVER J.E. & CLEMENTS F.E. 1938. Plant ecology. McGraw-Hill, New York.

WELLS P.V. 1965. Scarp woodlands, transported grassland soils, and concept of grassland climate in the Great Plains Region. Science 148:246-249.

WELLS P.V. 1970. Postglacial vegetation history of the Great Plains. Science 157:1574-1582.

WESTOBY M. 1974. An analysis of diet selection by large generalist herbivores. Am. Nat. 108:290-304.

WHITE F. 1983. The vegetation of Africa. A descriptive memoir to accompany the Unesco/AETFAT/UNSO vegetation map of Africa. Unesco, Paris.

WHITE R.E. & GROSSMAN D. 1972. The effect of prolonged seasonal burning on soil fertility under *Trachypogon* - other species of grassland at Frankenwald. S. Afr. J. Sci. 68:234-239.

WHITTAKER R.H. 1975. Communities and ecosystems 2nd ed. Macmillan, New York.

WHITTAKER R.H. & GOODMAN D. 1979. Classifying species according to their demographic strategy. I. Population fluctuations and environmental heterogeneity. Am. Nat. 113:185-200.

WONG S.C., COWAN I.R. & FARQUHAR G.D. 1979. Stomatal conductance correlates with photosynthetic capacity. Nature 282:424-426.

WOODWARD F.I. 1987. Climate and plant distribution. Cambridge University Press, Cambridge

ZACHARIAS P.J.K. 1990. The seasonal patterns in plant quality in various ecological zones in Natal. MSc (Agric.) thesis, University of Natal, Pietermaritzburg.

ZUCCHINI W. & ADAMSON P.T. 1984. The occurrence and severity of droughts in South Africa. Report to the Water Research Commission and the Department of Water Affairs. WRC Report No. 91/1/84.

ZUCCHINI W., ADAMSON P.T. & MCNEILL L. 1992. A model of southern African rainfall. S. Afr. J. Sci. 88:103-109.

APPENDIX 1

Weather Bureau station numbers (SNO), and names (STATION) of climate stations from different biomes (BT), used in the differentiation of South Africa's biomes as mapped by Rutherford & Westfall (1986). The latitude (LATIT) and longitude (LONGIT) of each station are provided (as degrees.minutes), and the values for each station of the following climatic indices are given (as ABBREVIATION; units): mean annual precipitation (PRECIPN; mm); growth temperature (GTEM; °C); no-growth temperature (NGTEM; °C), mean annual temperature (ANNT; °C), duration of the growth season (GDAYS; days).

ENO	BT	STATION	SNO	LATIT	LONGI	PRECPN	GTEM	NGTEM	ANNT	GDAYS
1	G	Volksrust	406	27.22	29.53	1024.7	16.9	13.2	14.7	146.4
2	G	Bloem (Tempe)	261	29.07	26.11	582.3	18.3	15.8	16.2	59.5
3	G	Kokstad	180	30.32	29.26	759.1	16.9	14.1	14.9	100.5
4	G	Queenstown	123	31.54	26.52	507.8	18.7	16.3	16.7	55.1
6	G	Vryheid	372	27.47	30.46	854.4	19.4	16.7	17.6	119.2
7	G	Pmburg PUR	239	29.36	30.26	965.1	20.6	16.9	18.2	125.6
8	G	Bethlehem	331	28.10	28.18	751.2	16.9	13.3	14.1	84.7
9	G	Lichtenburg	472	26.09	26.10	606.1	19.7	16.4	17.0	67.5
10	G	Carletonville	474	26.20	27.23	713.1	18.8	15.4	16.1	79.3
11	G	Krugersdorp	475	26.06	27.46	789.9	18.0	14.7	15.6	101.9
12	G	Zuurbekom	475	26.18	27.48	651.8	18.1	14.4	15.2	76.9
13	G	Bethal	478	26.27	29.29	634.0	17.6	14.4	15.1	79.9
14	G	Carolina	480	26.04	30.07	737.8	17.2	14.1	15.0	102.0
15	G	Gemsbokfontein	516	25.45	29.40	716.7	17.2	13.7	14.5	86.1
16	G	Belfast	517	25.39	30.02	614.4	16.0	13.0	13.7	89.7
17	G	Lydenburg	554	25.06	30.28	670.4	18.6	15.4	16.2	92.7
18	G	Bergvliet	555	25.04	30.53	1289.2	19.4	17.0	18.5	226.0
19	G	Jan Smuts	476	26.08	28.14	694.3	18.0	15.2	15.9	95.7
20	G	Zwartkopjes	476	26.21	28.04	733.9	18.8	14.9	15.8	81.0
21	G	Joubert Park	476	26.12	28.03	820.0	18.5	15.4	16.3	109.4
34	G	Dundee	335	28.10	30.14	813.7	19.2	16.1	17.0	106.2
35	G	Potchefstroom	437	26.44	27.05	600.6	19.9	16.6	17.1	58.5
36	G	Rietkuil	332	28.10	28.43	645.6	16.2	13.2	13.8	74.0
37	G	Doornlaagte	435	26.37	26.06	587.7	19.3	16.0	16.6	64.1
38	G	Whites	329	28.01	27.01	530.6	19.2	16.1	16.5	51.7
39	G	Jessievale	481	26.14	30.31	903.4	16.2	12.8	14.0	125.8
40	G	Virginia	328	28.06	26.52	519.8	19.3	16.5	16.9	54.8
41	G	Middelburg	515	25.46	29.28	701.3	18.4	14.7	15.5	80.2
42	G	Irene	513	25.55	28.13	939.6	18.9	15.6	16.7	119.0
43	G	Rietvlei	513	25.51	28.18	662.6	19.0	15.4	16.2	80.9
44	G	Estcourt TNK	300	29.00	29.53	754.9	19.2	16.1	16.9	94.2
45	G	Vereeniging	438	26.41	27.55	696.1	19.3	15.9	16.6	75.4
46	G	Melmoth	303	28.35	31.24	796.9	20.4	18.5	19.1	121.3
47	G	Standerton	441	26.56	29.14	649.5	17.7	14.3	15.0	77.1
48	G	Estcourt AGR	268	29.01	29.52	754.9	19.0	16.0	16.8	95.6
49	G	Nooitgedacht	442	26.31	29.58	736.0	16.8	13.7	14.5	98.0

APPENDIX 1 (cont.)

ENO	BT	STATION	SNO	LATIT	LONGI	PRECPN	GTEM	NGTEM	ANNT	GDAYS
50	G	Nottingham Rd	268	29.22	29.59	900.6	16.0	12.4	13.7	132.0
51	G	Piet Retief	444	27.00	30.48	745.5	18.6	16.0	16.7	102.7
52	G	Cherry Farm	296	28.52	27.51	777.1	17.3	13.9	14.8	93.8
53	G	Frankfort	403	27.16	28.30	667.5	18.2	14.4	15.2	75.9
54	G	Cathedral Pk	299	28.59	29.14	1386.0	14.6	12.3	14.0	268.9
55	G	Wakkerstroom	407	27.21	30.09	797.1	15.8	12.7	13.6	106.8
56	G	Glen College	293	28.57	26.20	577.8	18.9	15.7	16.2	55.7
57	G	Paulpietersburg	408	27.25	30.49	829.8	19.1	16.3	17.2	119.8
58	G	JBM Hertzog	261	29.06	26.18	540.8	18.4	15.3	15.8	55.2
59	G	Welkom	364	28.00	26.40	498.6	20.0	16.9	17.3	48.3
60	G	Rusfonteindam	262	29.16	26.36	562.8	18.3	15.5	16.0	60.5
61	G	Kroonstad MUN	365	27.40	27.15	582.1	19.4	16.1	16.6	54.0
62	G	Modderpoort	263	29.06	27.27	699.5	17.1	14.0	14.7	78.9
63	G	Lindley	366	27.53	27.55	638.1	18.2	14.8	15.4	64.4
64	G	Sheeprun	178	30.59	28.23	735.7	17.8	14.8	15.6	98.9
65	G	Newcastle	370	27.44	29.55	1322.7	19.8	15.4	17.5	172.3
66	G	Willow Park	148	31.30	26.57	507.4	16.2	14.1	14.5	70.1
171	G	Cathcart	101	32.17	27.09	554.0	16.5	14.5	14.9	77.2
172	G	Idutywa	103	32.06	28.18	723.2	17.7	16.2	16.7	121.0
22	S	Komatipoort	557	25.26	31.57	589.9	25.4	22.6	23.1	68.4
23	S	Nelspruit	555	25.26	30.59	789.2	22.3	19.0	20.0	108.2
24	S	Pretoriuskop	556	25.10	31.16	725.3	22.9	20.4	21.1	98.7
25	S	Zeerust	509	25.33	26.05	573.4	21.7	18.0	18.5	50.9
26	S	Rustenburg	511	25.43	27.18	774.5	21.5	17.5	18.5	88.5
27	S	Buffelspoort	511	25.45	27.29	688.0	21.3	18.0	18.7	74.1
28	S	Britz	512	25.35	27.49	619.0	21.6	17.9	18.5	62.2
29	S	Roodeplaat	513	25.35	28.21	664.3	21.0	17.4	18.1	73.0
30	S	Marico	546	25.30	26.21	613.5	22.4	19.0	19.6	62.3
31	S	Lindleyspoort	547	25.29	26.42	625.5	21.2	18.2	18.8	74.3
32	S	Saulspoort	548	25.10	27.10	613.4	22.5	18.7	19.4	64.9
33	S	Loskop	552	25.24	29.22	554.7	23.0	20.4	20.8	61.7
67	S	Muden	301	28.57	30.22	716.7	20.8	18.2	18.9	93.3
68	S	Kimberley	290	28.48	24.46	403.6	20.7	18.1	18.4	36.1
69	S	Koopmansfontein	323	28.12	24.04	339.7	19.4	16.6	16.8	30.7
70	S	Kuruman	393	27.28	23.26	445.1	20.1	17.4	17.7	44.3
71	S	Vaalharts	360	27.57	24.50	473.2	21.2	18.2	18.5	40.1
72	S	Sishen	356	27.47	22.59	387.6	22.1	18.8	19.1	37.2
73	S	Balkfontein	399	27.24	26.30	532.1	20.6	17.1	17.6	52.4
74	S	Ndumu	447	26.55	32.19	636.0	24.5	22.4	22.9	91.9
75	S	Armoedsvlakte	432	26.57	24.38	460.7	20.9	17.5	17.9	42.7
76	S	Mafikeng	508	25.51	25.39	570.3	21.5	18.1	18.6	56.7
77	S	Rooibokkop	591	24.53	29.22	609.1	23.5	19.6	20.2	58.5
78	S	Towoomba	589	24.54	28.20	572.2	21.9	18.3	18.9	61.1
153	S	Potgietersrus	634	24.11	29.01	591.3	22.3	19.0	19.6	70.0
154	S	Pietersburg	677	23.52	29.27	473.2	20.8	17.6	18.1	57.6
155	S	Chester	680	23.47	30.56	549.8	24.1	20.9	21.5	66.7
156	S	Phalaborwa	681	23.56	31.09	454.0	24.5	21.8	22.2	58.2

APPENDIX 1 (cont.)

ENO	BT	STATION	SNO	LATIT	LONGI	PRECPN	GTEM	NGTEM	ANNT	GDAYS
157	S	Marnitz	719	23.09	28.13	380.9	23.7	20.3	20.7	39.5
158	S	Mara	722	23.09	29.34	528.0	22.3	19.0	19.6	63.8
159	S	Levubu	723	23.05	30.17	1287.4	21.6	19.4	20.7	212.7
160	S	Gooldville	766	22.53	30.29	1068.3	22.3	20.2	21.2	175.0
161	S	Thabazimbi	587	24.37	27.24	608.5	23.7	20.5	21.1	64.8
165	S	Grahamstown	57	33.18	26.32	694.7	18.5	16.4	16.4	120.7
167	S	Somerset East	76	32.44	25.35	604.3	18.0	17.2	17.4	84.1
168	S	Lovedale	78	32.46	26.50	516.1	18.7	17.6	17.8	64.3
169	S	Kingwilliamst	79	32.52	27.24	534.1	19.0	17.6	17.9	77.8
79	K	Andriesfontn	171	30.57	24.36	319.1	16.8	14.6	14.8	32.3
80	K	De Aar	170	30.39	24.01	280.1	17.8	16.3	16.4	25.0
81	K	Bethulie	201	30.30	25.58	404.5	18.1	15.7	16.0	41.8
82	K	Fauresmith	229	29.46	25.19	418.7	17.8	15.5	15.8	42.3
83	K	PK LeRoux Dam	228	30.00	24.44	350.8	20.5	18.8	19.0	33.3
84	K	Kalkfontndam	259	29.30	25.13	351.7	20.1	17.7	17.9	33.1
85	K	Drieplotte	258	29.03	24.38	344.0	19.7	16.8	17.1	32.3
86	K	Rietrivier	258	29.07	24.36	375.2	19.9	17.3	17.5	32.3
87	K	Oviston	173	30.42	25.46	400.1	17.7	15.8	16.0	41.6
88	K	Burgersdorp	174	31.00	26.20	573.4	16.6	14.4	14.8	63.8
89	K	Aliwal North	175	30.43	26.43	495.4	17.9	15.4	15.7	49.8
90	K	Victoria West	141	31.24	23.09	218.6	16.3	14.8	14.9	19.4
91	K	GrootfonteinI	145	31.29	25.02	302.8	16.2	14.4	14.5	29.3
92	K	GrootfontnII	145	31.29	25.02	302.8	16.7	15.0	15.1	28.9
93	K	HF Verwoerd I	172	30.37	25.30	395.8	18.4	17.2	17.3	41.4
94	K	HF VerwoerdII	173	30.38	25.31	395.8	18.8	16.4	16.7	43.4
130	K	VanWyksvlei	193	30.21	21.49	147.4	19.1	18.2	18.2	12.8
131	K	Prieska	224	29.40	22.45	198.5	21.7	19.0	19.1	15.4
132	K	Britstown	169	30.35	23.31	227.0	18.4	17.0	17.1	21.4
133	K	Brandvlei	190	30.28	20.29	131.5	18.3	17.6	17.6	12.6
134	K	Williston	136	31.20	20.55	133.7	17.1	16.6	16.6	14.2
135	K	Carnarvon	165	30.58	22.00	199.5	16.4	15.9	15.9	27.5
136	K	Kenhardt	251	29.21	21.09	164.5	22.1	19.5	19.6	12.7
137	K	Boegoebergdam	253	29.03	22.13	197.2	22.5	20.1	20.2	17.5
138	K	Kareekloof	225	29.49	23.23	277.0	20.8	18.9	19.0	24.9
139	K	Pofadder	247	29.08	19.23	67.0	19.3	18.4	18.4	6.0
141	K	Sutherland	88	32.23	20.40	164.0	14.3	11.9	12.1	23.5
142	K	Beaufort West	92	32.21	22.35	225.3	18.3	17.5	17.6	25.6
143	K	Nelspoort	93	32.05	23.01	254.8	17.7	16.3	16.4	26.2
144	K	Graaff Reinet	96	32.15	24.32	339.3	19.0	18.3	18.4	38.0
145	K	Fraserburg	113	31.55	21.31	176.5	15.7	15.1	15.1	16.9
164	K	Willowmore	50	33.17	23.30	218.9	16.7	15.9	16.0	26.9
166	K	Jansenville	74	32.56	24.40	256.6	20.0	18.7	18.8	26.0
170	K	Cradock	98	32.10	25.37	320.5	18.3	16.4	16.6	34.8
95	T	Knysna	14	34.03	23.03	920.3	16.8	17.1	16.9	229.6
96	T	StormsRivMth	15	34.02	23.54	1109.4	16.4	16.4	16.4	364.0
126	T	Diepwalle	30	33.57	23.10	1154.8	15.5	14.8	15.4	315.8
97	F	CapeStFrancis	17	34.12	24.50	488.4	16.7	17.4	17.1	166.6

APPENDIX 1 (cont.)

ENO	BT	STATION	SNO	LATIT	LONGI	PRECPN	GTEM	NGTEM	ANNT	GDAYS
98	F	Danger Point	1	34.27	19.18	529.5	15.2	17.4	16.1	213.2
99	F	Cape Agulhas	3	34.50	20.01	469.7	15.7	17.9	16.9	167.7
100	F	Cape Point	4	34.21	18.30	595.2	14.7	17.4	15.6	243.1
101	F	Tokai	4	34.03	18.25	1136.1	15.8	19.1	16.3	309.5
102	F	Somerset West	5	34.05	18.49	607.3	14.8	19.0	17.0	173.2
108	F	CapeStBlaize	12	34.11	22.09	475.0	18.2	17.5	17.7	118.1
109	F	Tygerhoek	7	34.09	19.54	415.1	15.0	17.4	16.9	78.4
110	F	Riversdale	10	34.06	21.16	416.7	16.5	17.6	17.4	71.2
111	F	Steenbras Dam	5	34.11	18.51	607.3	13.5	18.1	15.7	188.8
112	F	Grabouw	6	34.09	19.02	1045.7	14.9	13.2	14.5	276.6
115	F	Wellington	21	33.38	19.00	660.1	14.7	20.2	18.1	139.6
116	F	Bien Donne	21	33.50	18.59	804.2	14.5	19.7	17.0	188.2
117	F	George	28	33.58	22.25	864.1	16.1	16.3	16.2	212.6
118	F	Grt Drakenstn	21	33.52	19.00	804.2	14.5	19.9	17.2	181.3
119	F	High Noon	22	33.55	19.18	716.2	13.0	16.6	14.7	193.2
120	F	Paarl	21	33.43	18.57	874.8	15.1	20.5	17.5	203.1
121	F	Welgevallen	21	33.56	18.52	723.7	14.1	18.6	16.4	179.9
122	F	Jonkershoek	21	33.58	18.56	1495.4	15.9	18.5	16.1	337.0
125	F	Heldervue	62	32.49	18.43	477.2	11.7	15.7	14.4	120.6
128	F	Saasveld	29	33.58	22.32	846.0	16.4	16.7	16.5	235.9
129	F	Langgewens	41	33.17	18.42	464.1	14.6	19.6	18.1	109.2
163	F	Matroosberg	43	33.26	19.49	275.1	11.4	14.8	14.4	46.3
113	U	Worcester	22	33.38	19.27	261.6	14.3	17.9	17.4	49.6
114	U	Montagu	24	33.47	20.07	171.6	15.7	17.7	17.6	25.9
140	U	Henkriesfontn	277	28.57	18.06	148.8	16.8	21.2	21.0	15.5
146	U	Vredendal	106	31.40	18.29	102.1	15.6	18.5	18.4	14.4
147	U	Klawer	107	31.47	18.37	365.4	16.4	19.9	19.3	66.5
148	U	Calvinia	134	31.28	19.46	254.1	13.3	16.8	16.4	39.3
149	U	Garies	157	30.34	18.00	130.9	15.9	19.0	18.9	16.8
150	U	Port Nolloth	242	29.14	16.52	75.9	13.6	14.5	14.4	28.4
151	U	Rietpoort	158	30.57	18.03	98.2	15.1	17.9	17.8	13.5
152	U	Okiep	214	29.36	17.52	213.5	14.2	18.0	17.7	32.8
162	U	Oudtshoorn	28	33.35	22.12	246.2	17.2	17.7	17.7	29.2

APPENDIX 2

A list of species abbreviations and species names used in the classification of woody vegetation units in the grassland biome. Species that were found in only one stand were omitted from the analysis. Nomenclature follows Gibbs Russell et al. (1987).

ACACATAX Acacia ataxacantha DC.
ACACKARR A. karoo Hayne
ACACSIEB A. sieberana DC.
ALOEFERO Aloe ferox Mill.
BRACDISC Brachylaena discolor DC.
BUDDSALI Buddleja saligna Willd.
CANTCILI Canthium ciliatum (Klotzsch) Kuntze
CANTINER C. inerme (L. F.) Kuntze
CLAUANIS Clausenia anisata (Willd.) Hook. F. ex Benth.
COMBMOLL Combretum molle R. Br. ex G. Don
CUSSPANI Cussonia paniculata Eckl. & Zeyh.
DIOSLYCI Diospyros lycioides Desf.
DIOSWEYT D. whyteana (Hiern) F. White
DOMBROTI Dombeya rotundifolia (Hochst.) Planch.
EHRIRIGI Ehretia rigida (Thunb.) Druce
EUCLCRIS Euclea crispa (Thunb.) Guerke
EUPHSPEC Euphorbia sp.
EURYSPEC Euryops sp.
FELIFILI Felicia filifolia (Vent.) Burtt Davy
FELIYELL Felicia sp.
GNIDHAIR Gnidia sp.
GREWOCCI Grewia occidentalis L.
HALLLUCI Halleria lucida L.
HETEARBO Heteromorpha trifoliata (Wendl.) Eckl. & Zeyh.
LEUCSERI Leucosidea sericea Eckl. & Zeyh.
LIPPSPEC Lippia sp.
MAYTHETE Maytenus heterophylla (Eckl. & Zeyh.) N.K.B. Robson
MAYTPOLY M. polyacantha (Sond.) Marais
MYRSAFRI Myrsine africana L.
OLEAAFRI Olea europaea L. subsp. africana (Mill.) P.S. Green
OSYRLANC Osyris lanceolata Hochst. & Steud.
PASSMONT Passerina montana Thoday
PAVESPEC Pavetta sp.
PROTCAFF Protea caffra Meisn.
RHUSDENT Rhus dentata Thunb.
RHUSEROS R. erosa Thunb.
RHUSLEPT R. leptodictya Diels
RHUSLUCI R. lucida L.
RHUSMACK R. rehmanniana Engl.
RHUSPYRO R. pyroides Burch.
RHUSSPIN R. longispina Eckl. & Zeyh.
SELASPEC Selago sp.
ZIZIMUCR Ziziphus mucronata Willd.

APPENDIX 3

Functional characters and attributes for each character, together with attribute scores. Abbreviations for each character are in parentheses.

Phenology (phn)	Physiology (phs)	Growth Form (gfm)	Reproduction (rep)
0 Unknown	0 Unknown	0 Unknown	0 Unknown
1 Annual	1 C3	1 Tufted	1 Oblig. veg.
2 Biennial	2 C4 NADP-ME	2 Stoloniferous	2 Veg & Sex
3 Perennial	3 C4 NAD-ME	3 Rhizomatous	3 Obl. seeder
4 Facult. Perenn	4 C4 PCK	4 All forms	
	5 C3 & C4	5 Tufted stolon.	
		6 Tufted rhizom.	

Seed size (ses)	Seed number (sen)	Seed Dispersal (sed)	Leaf pubescence (lpu)
0 Unknown	0 Unknown	0 Unknown	0 Unknown
1 Small	1 Many	1 Awned	1 Glabrous
2 Medium	2 Average	2 Non-awned	2 Slightly hairy
3 Large	3 Few	3 Barbed/hooked	3 Moderately hairy
		4 Plumed	4 Densely hairy

Leaf position (lpo)	Height (hgh)	Flowering time (ant)	Leaf length (lle)
0 Unknown	0 Unknown	0 Unknown	0 Unknown
1 Strongly basal	1 0 - 100mm	1 Early	1 To 10cm
2 Moderately basal	2 100 - 500mm	2 Early-middle	2 To 25cm
3 Few raised	3 500 - 1000mm	3 Middle	3 To 50cm
4 Many raised	4 > 1000mm	4 Middle-late	4 To 100cm
		5 Late	
		6 Early-mid-late	

Leaf x/s shape (lxs)	Leaf width (lwi)	Defence (def)	Woodiness (woo)
0 Unknown	0 Unknown	0 Unknown	0 Unknown
1 Expanded	1 To 3mm	1 None	1 Absent
2 Slighty folded	2 To 5mm	2 Growth form	2 Slight
3 Strongly folded	3 To 8mm	3 Wiregrass	3 Moderate
4 Slightly rolled	4 To 12mm	4 Turpenes	4 Strong
5 Strongly rolled	5 To 20mm	5 Tannins	
		6 Mtshiki	
		7 Other	

Geophytism (gph)	Palatability (pal)
0 Unknown	0 Unknown
1 Absent	1 Unpalatable
2 Slight	2 Sour
3 Moderate	3 Intermediate
4 Strong	4 Sweet
	5 Mtshiki

APPENDIX 4

Attribute scores for each functional character for each species ('co' is the species name abbreviation). This matrix was used to identify major functional features of South Africa's grassland biome. Characters are listed across the top of the table (cf. APPENDIX 3 for character names, and for attributes corresponding to each score).

Species name	co	phn	phs	gfm	rep	ses	sen	sed	lpu	lpo	hgh	ant	lle	lxs	lwi	def	woo	gph	pal
Alloteropsis semialata	as	3	5	1	3	3	3	2	4	2	3	6	3	1	4	7	2	4	2
Andropog appendiculat	aa	3	2	1	3	2	2	1	1	3	3	4	3	2	3	5	2	2	2
Andropogon schirensis	ah	3	2	1	3	2	2	1	2	3	3	4	4	2	5	5	2	2	2
Anthephora pubescens	ap	3	2	1	3	3	3	4	1	2	4	4	2	3	2	2	4	1	4
Aristida adscensionis	ar	1	2	1	3	1	1	1	1	4	3	4	3	5	1	3	2	1	1
Aristida bipartita	ab	4	2	1	3	1	1	1	1	3	2	4	2	5	1	3	2	1	1
Aristida congesta	ac	4	2	1	3	1	1	1	1	4	3	4	2	5	1	3	2	1	1
Aristida diffusa	ad	3	2	1	3	2	1	1	1	3	3	4	3	5	1	3	3	1	1
Aristida junciformis	aj	3	2	1	3	1	1	1	1	4	3	4	3	5	1	3	2	1	1
Aristida stipitata	ai	3	2	1	3	1	1	1	1	4	4	4	2	5	1	3	1	1	1
Aristida transvaalens	at	3	2	1	3	1	1	1	1	4	3	4	2	5	1	3	2	1	1
Bewsia biflora	bb	3	3	1	3	2	2	2	1	2	3	4	3	4	2	2	2	3	0
Bothriochloa insculpta	bi	3	2	5	2	2	1	1	2	3	4	4	3	2	3	5	2	2	3
Brachiaria eruciformis	be	1	4	6	2	1	2	2	1	3	2	6	2	4	3	2	1	1	4
Brachiaria nigropedata	bn	3	4	1	2	2	3	3	4	2	3	4	3	4	4	7	3	3	3
Brachiaria serrata	bs	3	4	1	3	2	3	3	4	4	3	4	2	4	4	7	2	4	3
Bromus catharticus	bu	4	1	1	3	2	2	2	1	3	3	6	1	2	3	1	1	1	4
Bromus sp.	br	1	1	1	3	0	0	2	0	2	2	0	0	0	0	0	0	0	4
Cymbopogon excavatus	ce	3	2	1	3	2	2	1	1	4	4	5	3	2	5	4	2	3	1
Cymbopogon plurinodis	cp	3	2	1	3	2	2	1	1	3	3	4	3	2	2	4	2	3	1
Cymbopogon validus	cv	3	2	1	3	2	2	1	2	4	4	4	4	2	4	4	2	3	1
Cynodon dactylon	cd	3	3	2	2	1	1	1	1	4	2	6	2	4	2	2	2	1	4

APPENDIX 4 (cont.)

Species name	hgh	ant	lle	lxs	lwi	co def	phn woo	phs gpb	gfm pal	rep	ses	sen	sed	lpu	lpo
Dichanthium annulatum	3	5	3	2	3	ds 5	3 2	2 2	1 0	3	2	3	1	2	3
Digitaria eriantha	4	4	3	2	4	de 1	3 3	2 1	6 4	2	2	2	2	2	2
Digitaria monodactyla	2	4	1	5	1	dm 7	3 2	2 3	1 3	2	2	4	3	2	2
Digitaria ternata	2	4	2	2	3	dt 1	2 1	1 1	1 4	3	1	1	2	2	4
Digitaria tricholaenoi	2	3	2	4	3	dr 2	3 2	3 3	6 4	2	3	3	4	4	1
Digitaria sp.(3)	0	0	0	0	0	d3 0	0 2	0 6	6 0	2	0	0	2	0	0
Diheteropogon amplect	4	5	3	2	5	da 5	3 2	2 3	1 3	3	2	2	1	1	3
Diheteropogon filifoli	2	6	3	5	2	df 5	3 2	2 3	1 1	3	2	2	1	1	2
Elionurus muticus	3	6	2	5	1	em 4	3 2	2 4	1 1	3	2	2	4	2	2
Eragrostis bicolor	2	4	2	5	2	ea 5	3 4	2 2	1 0	3	1	1	2	1	2
Eragrostis capensis	3	6	3	2	2	ec 5	3 3	2 3	1 3	3	1	2	2	2	2
Eragrostis chloromelas	3	4	2	5	1	eh 6	3 3	3 3	1 3	3	1	1	2	1	2
Eragrostis curvula	2	6	3	5	1	eb 6	3 3	3 3	1 3	3	1	1	2	1	2
Eragrostis gummiflua	3	4	3	4	2	eg 3	3 4	2 2	1 1	3	1	2	2	1	2
Eragrostis lehmanniana	3	4	2	5	1	el 3	3 4	2 2	6 3	2	1	1	2	1	4
Eragrostis obtusa	2	4	2	4	2	eo 2	3 2	2 2	1 0	3	1	1	2	1	3
Eragrostis pallens	4	4	4	4	3	eq 3	3 4	2 2	1 3	3	1	1	2	1	2
Eragrostis patentissim	3	4	4	4	0	et 5	3 4	3 2	6 0	2	1	1	2	1	3
Eragrostis plana	3	6	4	5	2	ep 6	3 2	2 2	1 1	3	1	1	2	1	2
Eragrostis racemosa	3	6	1	2	2	er 5	3 4	2 3	1 3	3	1	2	2	2	2
Eragrostis rigidior	3	4	2	4	2	ei 3	3 4	3 2	1 3	3	1	1	2	2	3
Eragrostis sclerantha	3	5	2	4	3	es 5	3 3	3 3	1 2	3	1	2	2	3	2
Eragrostis stapfii	3	4	2	5	1	ek 0	3 3	3 2	1 0	3	1	2	2	1	2
Eragrostis superba	3	6	3	2	4	eu 3	3 3	3 2	1 3	3	1	2	2	1	2
Eragrostis truncata	2	4	1	4	1	en 2	3 2	3 3	6 0	2	1	1	2	1	1

APPENDIX 4 (cont.)

Species name	co	phn	phs	gfm	rep	ses	sen	sed	lpu	lpo
hgh ant lle lxs lwi	def	woo	gph	pal						
Eulalia villosa	ev	3	2	1	3	2	2	1	4	3
4 6 2 1 3	5	3	3	2						
Eustachys paspaloides	ey	3	4	6	2	1	2	2	1	2
3 6 2 3 3	2	3	3	4						
Festuca caprina	fb	3	1	1	3	2	2	2	1	2
3 2 2 5 1	6	2	4	1						
Festuca costata	fc	3	1	1	3	2	2	2	1	2
4 2 4 4 3	6	2	4	1						
Festuca scabra	fs	3	1	1	3	2	2	2	1	2
3 2 3 4 4	6	2	4	1						
Harpochloa falx	hf	3	3	1	3	2	2	2	1	2
3 6 2 4 3	3	3	3	2						
Heteropogon contortus	hc	3	2	1	3	3	3	1	1	2
3 6 3 3 3	5	3	3	3						
Hyparrhenia hirta	hh	3	2	1	3	3	2	1	2	4
3 6 2 2 2	5	3	2	2						
Helictotrichon hirtulu	hs	4	1	1	3	2	2	1	1	3
3 4 2 1 3	0	1	1	4						
Karroochloa purpurea	kp	3	1	1	3	1	1	1	4	1
2 2 2 5 2	2	1	1	0						
Koeleria capensis	kc	3	1	1	3	1	1	2	2	2
3 2 1 5 1	7	2	3	3						
Lophacme digitata	ld	3	3	6	2	1	2	1	1	3
2 5 1 4 1	0	0	0	0						
Loudetia simplex	ls	3	2	1	3	2	2	1	4	2
4 6 3 4 2	5	2	3	2						
Melica decumbens	md	3	1	1	3	2	2	4	1	4
2 0 2 4 2	7	2	2	1						
Melinis nerviglume	rs	3	4	1	3	2	2	4	1	2
3 6 3 4 2	0	2	3	3						
Melinis repens	rr	4	4	1	3	2	1	4	3	2
3 6 2 1 3	0	1	1	3						
Microchloa caffra	mc	3	3	1	3	1	2	2	1	1
2 3 1 5 1	2	2	3	3						
Monocymbium ceresiifor	mo	3	2	1	3	2	2	2	1	3
3 5 2 2 3	5	2	3	3						
Merxmuellera disticha	mx	3	1	1	3	2	2	1	1	2
3 6 3 5 2	3	4	2	1						
Panicum coloratum	pc	3	3	1	3	2	2	2	2	3
3 4 3 2 4	5	3	2	4						
Panicum ecklonii	pe	3	1	1	3	2	2	2	4	2
3 2 2 2 3	0	2	3	0						
Panicum lanipes	pl	3	4	1	3	2	2	2	3	3
3 6 3 0 3	0	2	2	0						
Panicum natalense	pn	3	1	1	3	2	2	2	1	3
3 4 3 5 2	3	2	3	2						
Paspalum dilatatum	pd	3	2	6	2	3	3	2	2	3
4 4 3 1 5	2	3	3	4						
Paspalum scorbiculatum	ps	3	2	4	2	3	3	2	2	4
2 4 2 2 3	2	2	2	4						

APPENDIX 4 (cont.)

Species name	co	phn	phs	gfm	rep	ses	sen	sed	lpu	lpo
hgh ant lle lxs lwi	def	woo	gph	pal						
Pentaschistis airoides	pa	2	1	1	3	1	1	1	3	3
2 4 1 4 1	2	2	2	0						
Poa binata	pb	3	1	6	2	1	1	2	2	2
2 6 2 2 2	0	1	2	0						
Rendlia altera	ra	3	3	1	3	2	2	2	1	2
2 2 2 4 1	3	2	3	2						
Schizachyrium jeffreys	sj	3	2	1	3	2	2	1	1	3
4 5 2 2 2	5	2	3	2						
Schizacarium sanguineu	se	3	2	1	3	2	2	1	2	4
4 4 3 3 3	5	2	3	2						
Setaria nigrirostris	sn	3	2	6	2	3	3	2	2	2
3 4 3 4 4	2	3	4	3						
Setaria pallide-fusca	sp	1	2	1	3	2	2	2	2	3
3 4 2 2 4	0	2	2	4						
Setaria sphacelata	ss	3	2	6	2	2	1	2	2	2
3 4 3 2 2	2	2	4	3						
Sporobolus africanus	sa	3	4	6	2	1	1	2	1	2
4 4 3 5 2	6	2	2	1						
Sporobolus fimbriatus	sf	3	4	6	2	1	1	2	1	2
4 4 3 4 2	5	3	2	0						
Sporobolus indicus	si	3	4	6	2	2	2	2	1	3
4 4 4 5 0	0	0	0	0						
Sporobolus pectinatus	so	3	4	6	2	2	2	2	2	1
3 3 3 4 3	2	3	2	0						
Sporobolus pyramidalis	sy	3	4	1	3	1	1	2	1	2
4 4 3 5 4	6	2	2	1						
Sporobolus stapfianus	st	3	4	1	3	1	2	2	1	1
2 4 2 5 1	6	0	0	0						
Stiburus alopecuroides	sl	3	4	1	3	2	2	4	4	2
3 6 3 5 1	5	2	3	2						
Tetrachne dregei	td	3	3	6	2	2	2	2	1	2
3 4 2 5 1	2	4	2	4						
Themeda triandra	tt	3	2	1	3	3	3	1	3	4
4 6 3 2 3	5	3	3	2						
Trachypogon spicatus	ts	3	2	1	3	3	3	1	3	3
4 4 2 4 2	5	2	3	2						
Tragus berteronianus	tb	4	3	1	3	2	2	3	2	4
2 4 1 1 2	2	1	1	4						
Tragus koelerοides	tk	3	3	4	2	2	2	3	2	3
2 6 1 1 1	2	2	1	4						
Trichoneura grandiglum	tg	1	3	1	3	1	1	2	2	4
2 4 2 2 3	0	1	2	4						
Triraphis andropogonoi	ta	3	3	3	2	2	2	1	1	3
3 4 3 4 4	5	4	3	1						
Tristachya leucothrix	tl	3	2	1	3	3	3	1	4	2
3 6 3 4 3	5	2	3	3						
Tristachya rehmannii	tr	3	2	1	3	3	3	1	4	2
3 4 2 4 1	7	3	2	1						
Urelytrum agropyroides	us	3	2	1	3	3	3	1	1	2
4 4 3 2 3	5	3	2	1						
Urochloa mossambicensi	um	3	4	5	2	3	3	2	2	4
4 4 3 2 5	2	3	3	4						

APPENDIX 5A

Scores for species on the first four axes of the detrended correspondence analysis.

SPECIES	AXIS 1	AXIS 2	AXIS 3	AXIS 4
AA	1	8	0.1	0.8
AB	0	-3	0	-0.3
AC	21	29	2.1	2.9
AD	13	-13	1.3	-1.3
AH	-23	1	-2.3	0.1
AI	31	34	3.1	3.4
AJ	7	-9	0.7	-0.9
AP	44	61	4.4	6.1
AR	-2	-6	-0.2	-0.6
AS	-31	-1	-3.1	-0.1
AT	-3	31	-0.3	3.1
BB	-9	3	-0.9	0.3
BE	2	2	0.2	0.2
BI	6	8	0.6	0.8
BN	27	45	2.7	4.5
BR	25	-29	2.5	-2.9
BS	6	8	0.6	0.8
BU	77	-74	7.7	-7.4
CD	37	44	3.7	4.4
CE	-4	5	-0.4	0.5
CP	13	3	1.3	0.3
CV	-3	1	-0.3	0.1
DA	1	5	0.1	0.5
DE	38	-36	3.8	-3.6
DF	-23	-1	-2.3	-0.1
DM	-3	3	-0.3	0.3
DR	-6	2	-0.6	0.2
DS	-2	6	-0.2	0.6
DT	4	6	0.4	0.6
EA	28	-35	2.8	-3.5
EB	5	5	0.5	0.5
EC	-4	-2	-0.4	-0.2
EG	29	56	2.9	5.6
EH	29	-24	2.9	-2.4
EI	56	91	5.6	9.1
EK	53	88	5.3	8.8
EL	46	67	4.6	6.7
EM	4	4	0.4	0.4
EN	42	-39	4.2	-3.9
EO	54	-44	5.4	-4.4
EP	5	0	0.5	0
EQ	20	16	2	1.6
ER	-8	3	-0.8	0.3
ES	-34	0	-3.4	0
ET	-6	1	-0.6	0.1
EU	20	25	2	2.5
EV	-32	-2	-3.2	-0.2
EY	12	18	1.2	1.8
FB	-37	-2	-3.7	-0.2
FC	-22	-3	-2.2	-0.3
FS	-12	-12	-1.2	-1.2
HC	-4	1	-0.4	0.1
HF	-10	1	-1	0.1
HH	-1	8	-0.1	0.8
HS	-9	0	-0.9	0
KC	-19	-2	-1.9	-0.2
KP	46	-48	4.6	-4.8
LD	-14	4	-1.4	0.4
LS	-29	0	-2.9	0
MC	-10	0	-1	0
MD	72	-69	7.2	-6.9

APPENDIX 5A (cont.)

SPECIES	AXIS 1	AXIS 2	AXIS 3	AXIS 4
MO	-23	1	-2.3	0.1
MX	42	-49	4.2	-4.9
PA	35	-40	3.5	-4
PB	2	-4	0.2	-0.4
PC	15	10	1.5	1
PD	2	7	0.2	0.7
PE	-32	-1	-3.2	-0.1
PL	-7	4	-0.7	0.4
PN	-14	3	-1.4	0.3
PS	-1	9	-0.1	0.9
RA	-19	-1	-1.9	-0.1
RB	5	3	0.5	0.3
RR	4	11	0.4	1.1
RS	-19	3	-1.9	0.3
SA	25	24	2.5	2.4
SE	-12	4	-1.2	0.4
SF	42	39	4.2	3.9
SI	-4	3	-0.4	0.3
SJ	-20	1	-2	0.1
SL	-38	0	-3.8	0
SN	-5	2	-0.5	0.2
SO	-5	3	-0.5	0.3
SP	-13	0	-1.3	0
SS	12	6	1.2	0.6
ST	-2	6	-0.2	0.6
SY	-1	9	-0.1	0.9
TA	37	60	3.7	6
TB	25	22	2.5	2.2
TD	35	-39	3.5	-3.9
TG	0	4	0	0.4
TK	13	16	1.3	1.6
TL	-11	0	-1.1	0
TR	-12	5	-1.2	0.5
TS	-13	3	-1.3	0.3
TT	-3	-4	-0.3	-0.4
UM	3	6	0.3	0.6
US	-15	2	-1.5	0.2
UX	5	3	0.5	0.3
VS	35	-40	3.5	-4
WA	4	2	0.4	0.2
WB	4	5	0.4	0.5
WC	-6	4	-0.6	0.4
WD	-5	3	-0.5	0.3
WE	-15	3	-1.5	0.3
WF	-13	6	-1.3	0.6
WG	-16	-1	-1.6	-0.1
WH	35	-40	3.5	-4
WJ	45	-50	4.5	-5
WK	38	-40	3.8	-4
WN	-4	6	-0.4	0.6
WT	-3	10	-0.3	1
WU	-22	0	-2.2	0
WV	-22	0	-2.2	0
WW	-19	-2	-1.9	-0.2
WX	2	-4	0.2	-0.4
WY	3	-2	0.3	-0.2
WZ	-30	-2	-3	-0.2
XE	40	7	4	0.7
XH	52	87	5.2	8.7
XJ	20	16	2	1.6
XP	-45	-2	-4.5	-0.2
XS	-45	-2	-4.5	-0.2
XT	-29	-1	-2.9	-0.1
XU	-36	1	-3.6	0.1
XV	-45	-2	-4.5	-0.2
D3	-13	6	-1.3	0.6

APPENDIX 5B

Scores for samples on the first four axes of the detrended correspondence analysis. Abbreviations for samples are as in Figure 6.1

SAMPLES	AXIS 1	AXIS 2	AXIS 3	AXIS 4
S1	260	-271	2.6	-2.71
S3	407	-454	4.07	-4.54
S4	567	-508	5.67	-5.08
S5	366	-379	3.66	-3.79
S6	312	-269	3.12	-2.69
S7	192	-174	1.92	-1.74
S8	345	-328	3.45	-3.28
S9	263	-268	2.63	-2.68
S10	210	-238	2.1	-2.38
R1	39	-23	0.39	-0.23
R2	14	-12	0.14	-0.12
R3	21	0	0.21	0
R4	-45	-39	-0.45	-0.39
R5	99	-92	0.99	-0.92
R6	73	-51	0.73	-0.51
R7	-39	-15	-0.39	-0.15
R8	-12	-16	-0.12	-0.16
R9	-37	-30	-0.37	-0.3
R10	8	-23	0.08	-0.23
R11	-27	-7	-0.27	-0.07
R12	-39	-34	-0.39	-0.34
R13	23	-57	0.23	-0.57
R14	154	-175	1.54	-1.75
R15	-223	-14	-2.23	-0.14
WAT1	-119	-10	-1.19	-0.1
WAT2	-160	0	-1.6	0
WAT3	-160	2	-1.6	0.02
WAT4	-155	2	-1.55	0.02
WAT5	-171	-7	-1.71	-0.07
WAT6	-81	-11	-0.81	-0.11
WAT7	47	23	0.47	0.23
WAT8	-45	-28	-0.45	-0.28
WAT9	-65	-12	-0.65	-0.12
WAT10	-117	-13	-1.17	-0.13
WAT11	-117	-12	-1.17	-0.12
WAT12	-105	-16	-1.05	-0.16
WAT13	-140	-4	-1.4	-0.04
E1	74	69	0.74	0.69
E2	-25	70	-0.25	0.7
E3	-45	24	-0.45	0.24
E4	21	87	0.21	0.87
E5	-46	7	-0.46	0.07
E6	-44	7	-0.44	0.07
E7	-11	-14	-0.11	-0.14
E8	19	44	0.19	0.44
P1	-15	41	-0.15	0.41
P2	72	63	0.72	0.63
P3	4	81	0.04	0.81
P4	16	69	0.16	0.69
P5	-26	44	-0.26	0.44
P7	-78	0	-0.78	0
P8	-89	17	-0.89	0.17
P9	-46	43	-0.46	0.43
WAK1	-61	-9	-0.61	-0.09
WAK2	-41	7	-0.41	0.07
WAK3	-29	18	-0.29	0.18
WAK4	30	19	0.3	0.19
WAK5	-25	7	-0.25	0.07
WAK6	39	22	0.39	0.22
WAK7	-50	15	-0.5	0.15
WAK8	-29	18	-0.29	0.18

APPENDIX 5B (cont.)

SAMPLES	AXIS 1	AXIS 2	AXIS 3	AXIS 4
WAK9	-28	21	-0.28	0.21
WAK10	-39	-4	-0.39	-0.04
WAK11	-10	28	-0.1	0.28
WOL1	316	435	3.16	4.35
WOL2	220	205	2.2	2.05
WOL3	346	216	3.46	2.16
WOL4	409	621	4.09	6.21
WOL5	126	11	1.26	0.11
WOL6	108	-13	1.08	-0.13
WOL7	296	50	2.96	0.5
WOL8	372	506	3.72	5.06
WOL9	151	109	1.51	1.09
WOL10	385	597	3.85	5.97
WOL11	103	163	1.03	1.63
M1	-146	6	-1.46	0.06
M2	-101	131	-1.01	1.31
M3	-50	24	-0.5	0.24
M4	-114	8	-1.14	0.08
M5	-96	42	-0.96	0.42
M6	-28	20	-0.28	0.2
M7	-4	45	-0.04	0.45
M8	-47	17	-0.47	0.17
M9	-110	14	-1.1	0.14
G1	-278	-8	-2.78	-0.08
G2	-332	-14	-3.32	-0.14
G3	-209	-17	-2.09	-0.17
G4	-214	-18	-2.14	-0.18
G5	-332	-15	-3.32	-0.15
G6	-300	-5	-3	-0.05
G7	-201	-5	-2.01	-0.05
G8	-214	-7	-2.14	-0.07
G9	-264	6	-2.64	0.06
G10	-329	-10	-3.29	-0.1
L1	-13	-19	-0.13	-0.19
L2	25	12	0.25	0.12
L3	48	25	0.48	0.25
L4	28	16	0.28	0.16
L5	31	34	0.31	0.34
L6	87	-6	0.87	-0.06
L7	33	45	0.33	0.45

Author: Ellery William Nolan.
Name of thesis: Classification of vegetation of the South African grassland biome.

PUBLISHER:
University of the Witwatersrand, Johannesburg
©2015

LEGALNOTICES:

Copyright Notice: All materials on the University of the Witwatersrand, Johannesburg Library website are protected by South African copyright law and may not be distributed, transmitted, displayed or otherwise published in any format, without the prior written permission of the copyright owner.

Disclaimer and Terms of Use: Provided that you maintain all copyright and other notices contained therein, you may download material (one machine readable copy and one print copy per page)for your personal and/or educational non-commercial use only.

The University of the Witwatersrand, Johannesburg, is not responsible for any errors or omissions and excludes any and all liability for any errors in or omissions from the information on the Library website.