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AN ECOLOGICAL STUDY OF THE VEGETATION OF EASTERN BUSHMANLAND (NAMIBIA) AND ITS IMPLICATIONS FOR DEVELOPMENT

Christopher John Henry Hines

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by

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B.Sc (Hons.) (Natal)

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ABSTRACT

The Kalahari Geological System, of south and central Africa, is well known for it's largely uniform overburden of aeolian sand. Eastern Bushmanland, the study area in northern Namibia, is atypical within the Kalahari System as there is extensive surficial exposure of the underlying geological strata. The resultant variation in soils and geomorphological features has given rise to a variety of habitats which is reflected in a diversity of vegetation types within a limited area.

Eighteen vegetation associations, identified by classification of Braun-Blanquet floristic data, are described. These associations compare closely to associations described elsewhere in southern Africa. The combined assemblage of species and associations is shown to be unique within the Kalahari System and showed greater species richness and diversity of associations than areas of comparable size within the Kalahari. The phytochorology of the region is discussed.

The ordination of both floristic data and soil physico-chemical data indicated a spatial pattern of small vegetation units influenced by soil physico-chemical variation and geomorphological landforms.

A model of the possible environmental determinants of the vegetation associations was constructed using the results of the classification and ordinations. Possible avenues for future research are outlined.

PREFACE

The work described in this thesis was carried out in Bushmanland (Namibia) and the Institute of Natural Resources (Pietermaritzburg) under the supervision of Professor C.M. Breen.

These studies represent original work by the author and have not been submitted in any form to another University. Where use was made of the work of others it has been duly acknowledged in the text.

I hereby declare that, except where otherwise stated, all material presented hereunder is original and has not been submitted for publication or any other purpose.

C.J.H. Hines

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CHAPTER ONE

INTRODUCTION

1.1 INTRODUCTION TO THE STUDY

That Africa is in a state of "ecological crisis" has become a truism in both the popular and scientific literature in recent years (Borgin & Corbett, 1982; Sinclair & Fryxell, 1985; Timberlake, 1985; Rosenblum & Williamson, 1987). The argument is given that Africa is entering an ever-steepening spiral of environmental degradation and desertification, as a rapidly growing human population subject to decreasing living standards, expands subsistence agriculture into marginal "unsuitable" lands and the natural resource base is rapidly degraded (Myers, 1984; Timberlake, 1985; Hanks, 1987; Anon., 1990). The validity of the argument is the subject of debate (Myers, 1984; Timberlake, 1985; Bell, 1987; Norton, 1988), but there is little doubt that, within the southern African context, there is an increasing demand for land as human populations increase and that large tracts of land becoming available or zoned for development, are situated in the semi-arid parts of the subcontinent.

There are a number of definitions for semi-arid regions usually based on accurate climatic delimitations (for example, Schulze & McGee, 1978). Walker (1979a), however, defines semi-arid regions as those where the climate is too dry and variable to permit regular, successful, annual dry-land cultivation of crops and so land-use is primarily based on utilization of the natural vegetation and associated wildlife.

Historically, these areas carried low human populations, generally peoples practising some form of nomadic life-style oriented around the exploitation of the seasonal resources in these areas (Walker, 1979a). However, human populations have become increasingly sedentary in arid and semi-arid areas of Africa as the provision of health services, food aid and other support programmes have broken down the requirement for a nomadic way of life. These populations have expanded rapidly and are often insufficiently subsidised by the aid programmes. The effect in many communities has been that the human population has increased past the carrying capacity of the primary resources on which the people depend. The resultant rapid deterioration of valuable indigenous resources such as woodlands, grazing and wildlife, leads to a downward spiral of environmental degradation, lowered carrying capacity, increased demand for aid and increased human suffering.

Semi-arid regions are perhaps more susceptible to rapid change than more mesic environments (Walker, 1979b; Griffin & Friedel, 1985). They are regarded by a number of authors as "fragile ecosystems" (Walker, 1979b; Pryor, 1982; Myers, 1984) and it is argued that these regions require "higher-than-average" management (Walker, 1979b). That these areas are frequently subjected to poor and indifferent management practices is largely as a consequence of a poor understanding of the limitations of the resource base and the environmental constraints on its utilisation. If development planning in rural areas is to be effective, it is essential to have a clear understanding of the resources and the environmental constraints operating on these resources.

The question of determining development options in rural areas is complex, but is one of considerable urgency in the face of increasing human populations and a diminishing resource base.

In considering the multifarious nature of the economic, social and ecological aspects of development options, points of conflict are raised. In rural areas previously undeveloped or with their wildlife populations intact, a recurrent point of conflict is that of wildlife conservation versus agricultural development (Anderson &

Grove, 1987; Lewis *et al.*, 1990; Barbier, 1992). Eastern Bushmanland (Figure 1.1), the study area in northern Namibia, is no exception.

Eastern Bushmanland is semi-arid (van der Merwe, 1983) and due to the limited nature of the natural resources in the area, the conflict between wildlife conservation and agricultural development is essentially dissension over the utilisation of the indigenous vegetation resources. However, eastern Bushmanland is exceptional in that the human population is low, not yet exceeding the carrying capacity. It may be possible to develop the area in a manner in which the population can sustain itself in the long term, both through utilisation of the wildlife resources and the development of a subsistence livestock industry.

Whatever development option (wildlife based, livestock based or a combination of both) is selected, in order to promote sound management and sustainable utilisation of the resource base, an inventory of the resources, an analysis of the ecological interrelationships in the area and an appraisal of the environmental constraints on the sustained utilization of the resources, is necessary.

The purpose of this study was to gain an understanding of the determinants of the composition, structure and distribution of the vegetation of eastern Bushmanland,

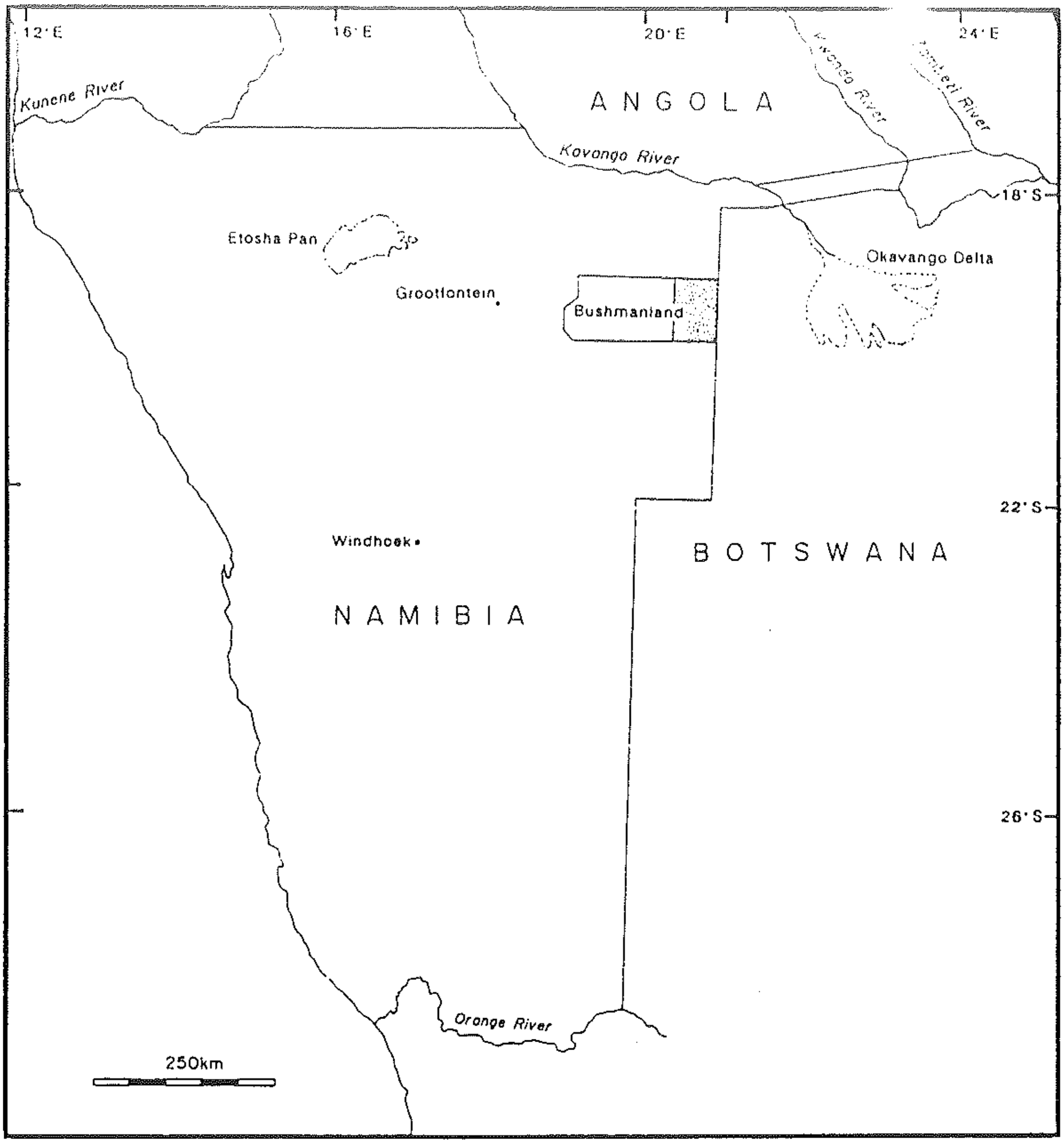


Figure 1.1 Map showing the position of Bushmanland and the study area (stippled) within Namibia.

Namibia. This was achieved through the survey and classification of the major vegetation units in the area and through the ordination of floristic and soils physico-chemical data. Development proposals for the area are discussed within the framework of what is known about the limitations of the resources and the environmental constraints on the utilisation and management of these resources.

CHAPTER TWO

THE STUDY AREA

2.1 INTRODUCTION

The vegetation of eastern Bushmanland reflects the interplay between processes occurring over long time scales of hundreds to thousands of years (such as climatic change, geological processes), as well as much shorter time scales ranging from a single event (such as fire) to several years (such as grazing intensity). Local abiotic factors are described here to provide a framework for the discussion of the importance of these factors in determining the vegetation associations and resources in eastern Bushmanland, and to allow comparisons to be made with other semi-arid systems.

2.2 GEOGRAPHIC POSITION AND EXTENT

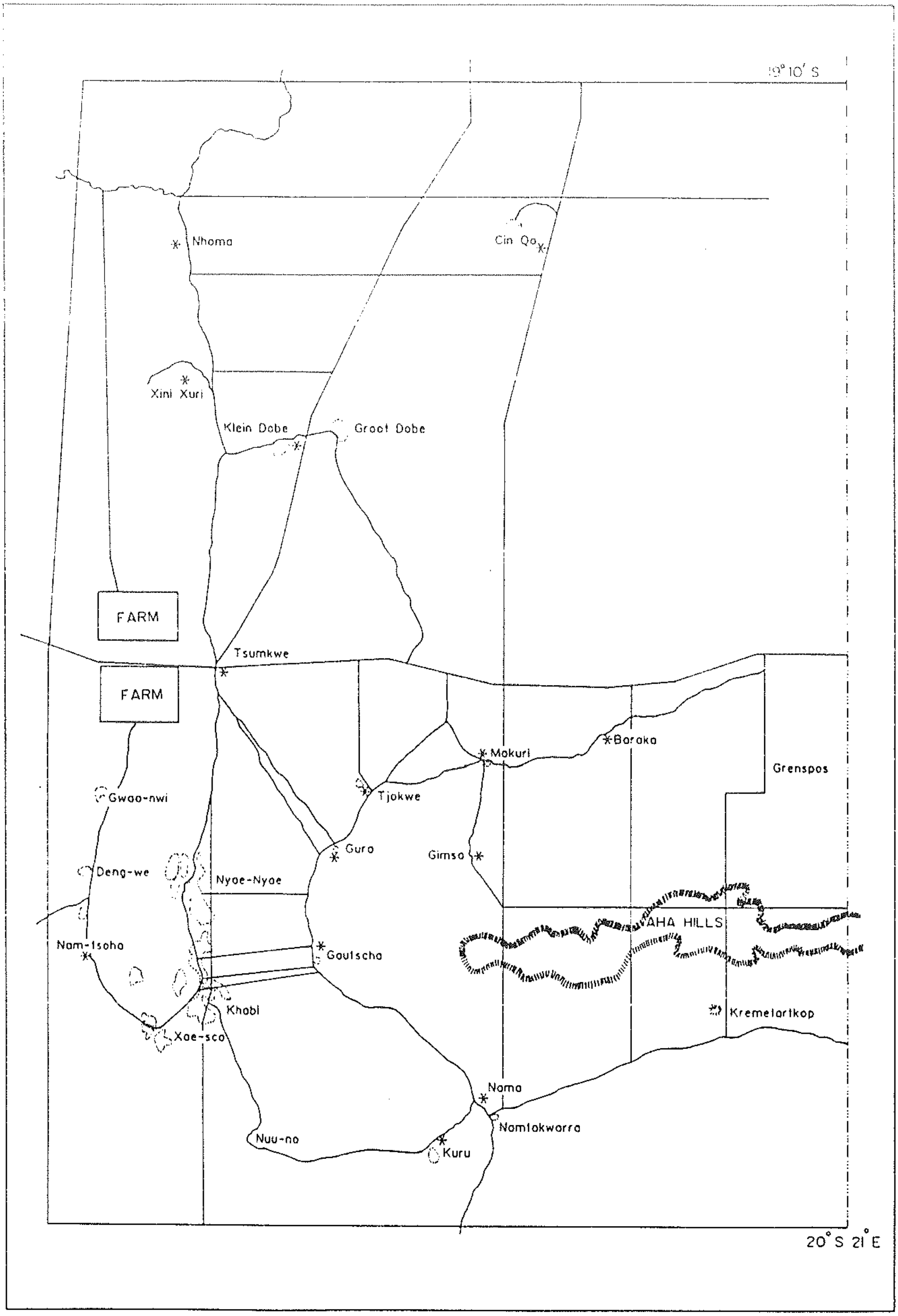
Bushmanland in north-eastern Namibia is an area of some two million hectares, the boundaries of which were determined by the Odendaal Commission of 1963 (Anon, 1964). The area was set aside as a "homeland" for the Bushman peoples of Namibia, in accordance with the apartheid policies of the South African administration of the time. All place names mentioned in the text are shown in Figure 2.1.

The study area comprises approximately 700 000 ha in eastern Bushmanland, (Figure 1.1). The boundaries of the study area shown in Figure 2.1, are those proposed for a possible National Park wildlife conservation area (Anon, 1983) to be developed by the then Directorate of Nature Conservation (now the Ministry of Wildlife, Conservation and Tourism).

2.3 GEOLOGY, GEOMORPHOLOGY AND SOILS

The study area falls within the Kalahari Geological System (Cooke, 1964), which extends through much of the western half of Africa (Figure 2.2). It is situated on a broad, flat watershed between the Nhoma and Daneib drainages (Ward & Swart, 1989) about 400 km north of the Bakalahari-Schwelle a low, west-east orientated ridge which divides the Kalahari into north and south drainages (Figure 2.2). The average altitude is *c.* 1010 m above mean sea level.

Figure 2.1 Map of eastern Bushmanland showing the boundaries of the study area, settlements (✱), roads, pans (◌) and the approximate extent of the Aha Hills (〰).


19° 10' S
Nhoma
Cin Qa
Xini Xuri
Klein Dobe
Groot Dobe
FARM
Tsumkwe
FARM
Baraka
Mokuri
Grenspos
Gwaa-nwi
Tjokwe
Guru
Gimsa
Deng-we
Nyae-Nyae
AHA HILLS
Nam-tsoha
Gautscha
Khabi
Kremetartkop
Xae-sca
Nama
Namtakwarra
Nuu-na
Kuru
20° S 21° E

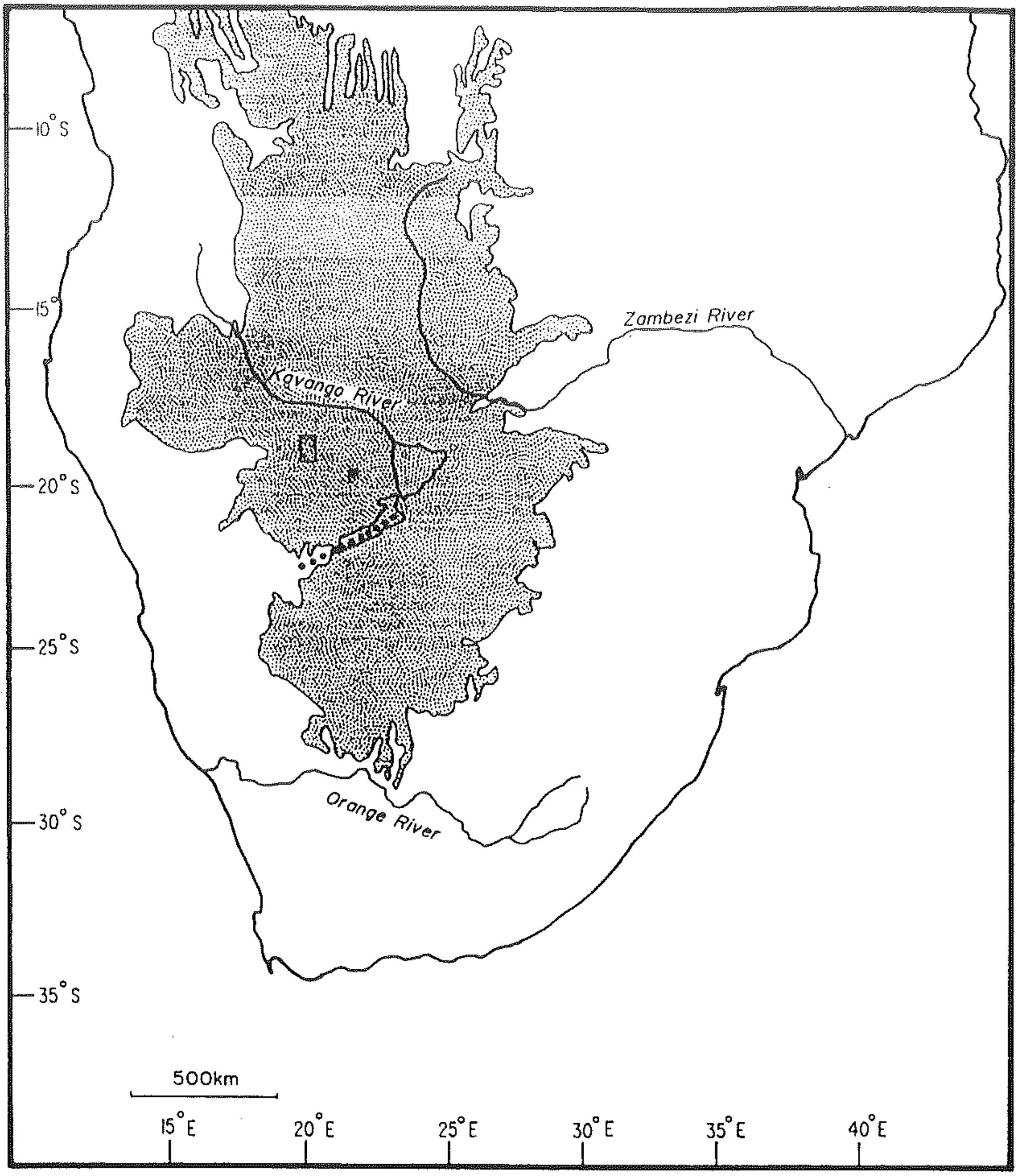


Figure 2.2 Map of southern Africa showing the approximate extent of the Kalahari Geological System (after Cooke, 1964) (shaded) and the postion of the study area (stippled) in relation to the Bakahalari-Schwelle (dotted line).

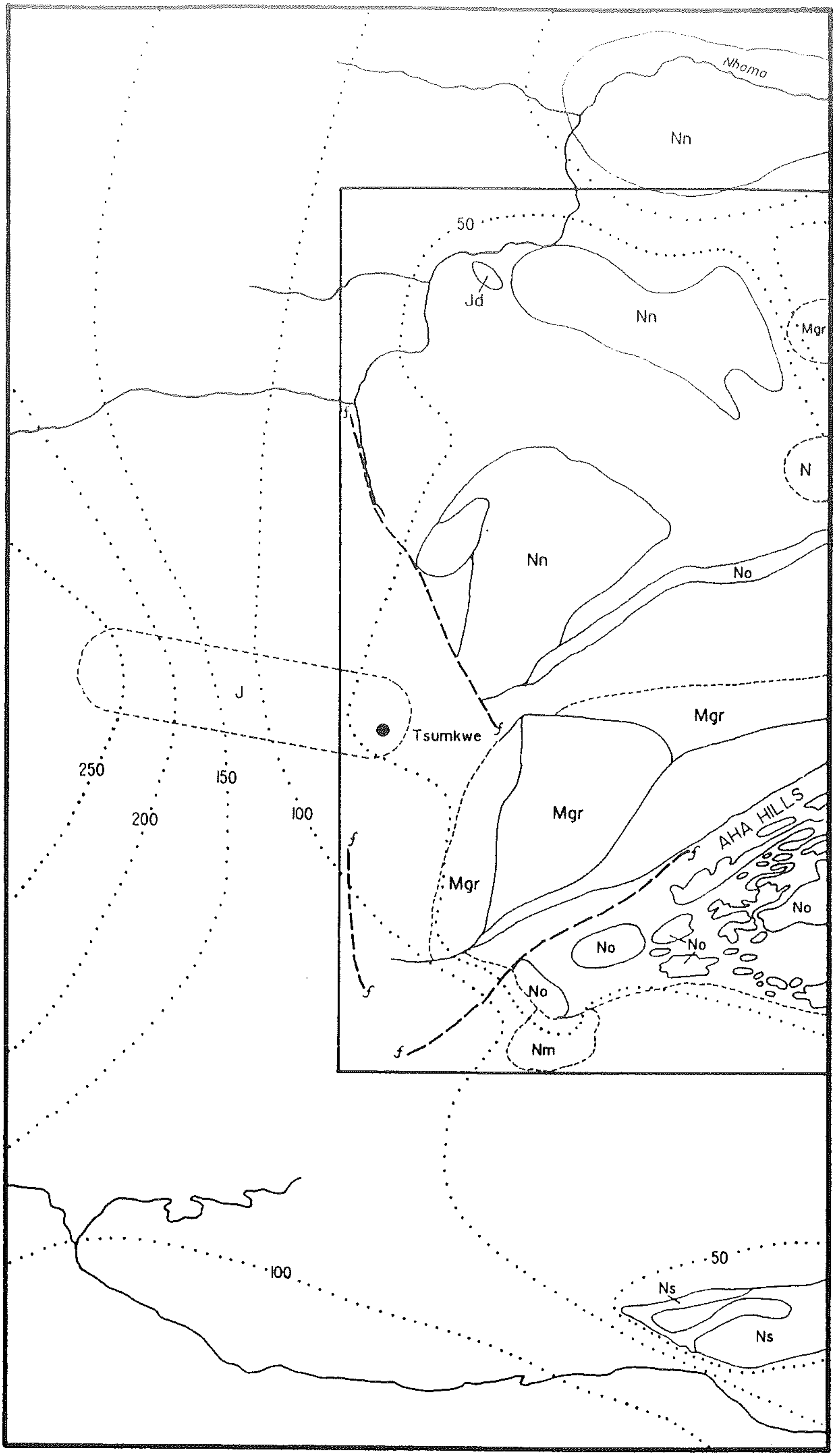
The Kalahari System is made up primarily of aeolian sand deposits and associated calcareous deposits (Cooke, 1964; Hegenberger, 1983; Thomas, 1988). These deposits obscure much of the basement geology and it is a feature of the Kalahari System that there is little surficial exposure of bedrock over much of its extent (Anon., 1980; Cole, 1986).

In eastern Bushmanland bedrock exposure is, however, widespread (Figure 2.3). This is as a consequence of the Aha Hills in the south-east of the study area acting as a barrier to sand transport, which significantly reduced the westward transport of aeolian sand by easterly winds during the Late Caenozoic (Baillieul, 1975; Ward & Swart, 1989). West of the Aha Hills the cover of surface sands is thin and in parts the wind action has developed large deflation surfaces in the landscape. Outcrops of early Precambrian granites are common east of Tsumkwe and in areas of shallow soil cover, subsurface features such as massive fracturing (Plate 2.1), are clearly discernible. To the north of Tsumkwe there is extensive exposure of Nosib quartzite of the Damara sequence (Hegenberger, 1983). These quartzites are widely distributed under a shallow cover of Kalahari sand. Structural features such as anticlinal and synclinal folds and faulted strata can be seen where certain vegetation units closely follow the structures (Plate 2.2). The Aha Hills comprise largely dolomites and stromatalithic limestones of the Otavi Group of the Damara sequence (Hegenberger, 1983).

Figure 2.3 Geological map of the area between the Nhoma and Daneib drainages, showing the boundaries of the study area and the extent of the different geological strata. Boundaries of sub-surficial deposits are indicated by broken lines. Scale 1:500 000.

Key:

...50.. = Depth contours of the Kalahari deposits
f-----f = Fault lines
Jd = Jurassic dolerite
Mgr = Granite
Nm = Mulden group phyllite, quartzite and conglomerate
Nn = Nosib group quartzite, conglomerate, schist and dolomite
No = Otavi group dolomite and limestone
Ns = Swakop group marble, schist and quartzite


Nhoma
Nn
50
Jd
Nn
Mgr
N
Nn
No
J
Tsumkwe
Mgr
250
150
100
200
Mgr
AHA HILLS
Mgr
No
No
No
No
Nm
100
50
Ns
Ns

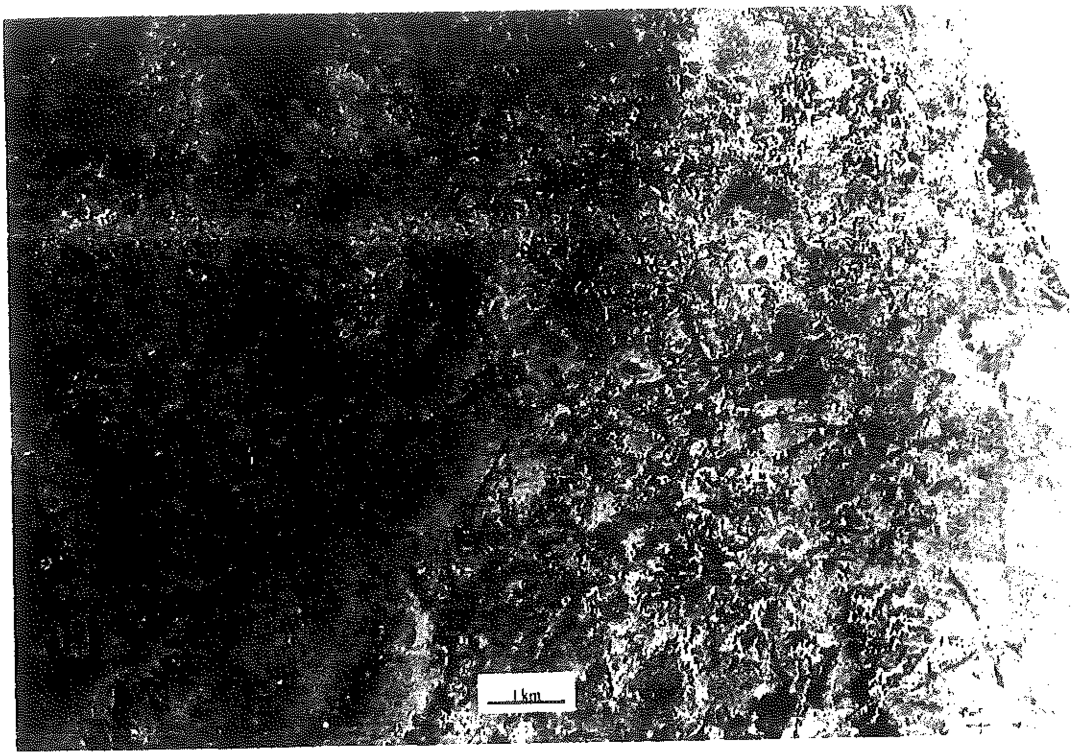


Plate 2.1 Aerial photograph of the Makuri area, east of Tsumkwe showing massive fracturing in the granite plates.

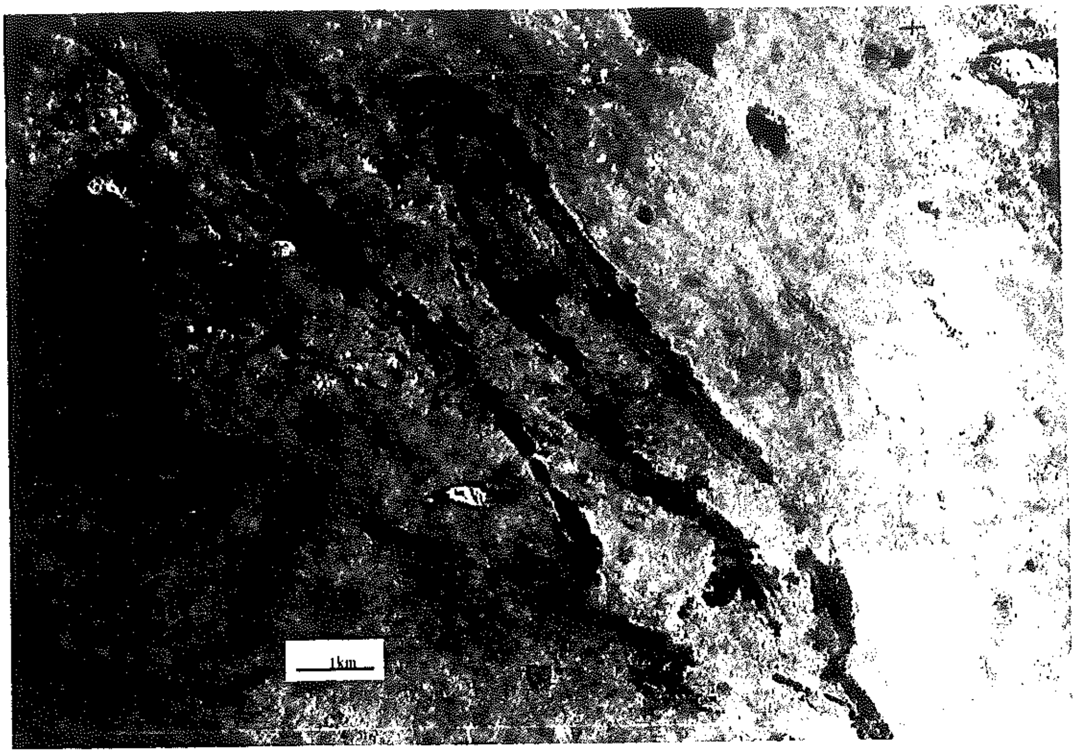


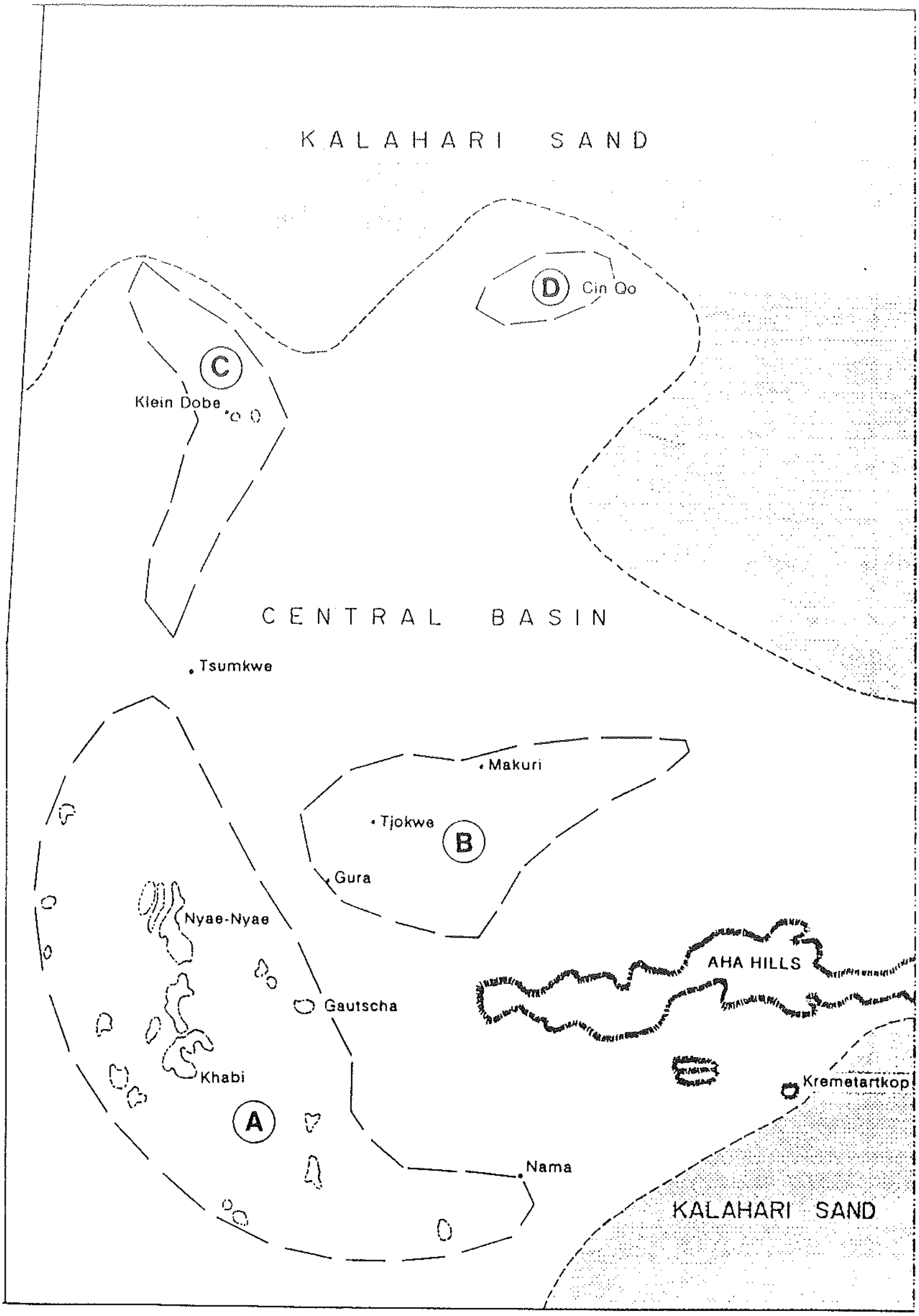
Plate 2.2 Aerial photograph of a large structural fold near Cin Qo, covered by a dense stand of *Terminalia prunioides*.

The importance of the surficial exposure of the basement geology lies in the effects this has had on soil formation. The breakdown of parent materials affects the nutrient status, texture and water holding capacity of a soil, all of which are important in determining the type of vegetation present in an area.

For ease of reference, the study area is broadly divided into the "Kalahari Sand" areas, where soils are deep (>1.5 m), unconsolidated aeolian sands, and the "Central Basin" where soils are predominantly shallow to moderately deep (0.1-1.5 m) litholitic soils. The approximate extent of these two areas is shown in Figure 2.4. West of the Aha Hills the widespread development of pedogenic calcretes, centred on the Nyae-Nyae area (Ward & Swart, 1989) and the erosional effects of palaeo-winds has promoted the formation of pans which act as foci of drainage. The extent of the major pan systems in eastern Bushmanland is shown in Figure 2.4. The Nyae-Nyae pans and associated woodlands comprising an area in excess of 100 000 ha, are extensively flooded during years of above average rainfall (Hines, in press). Pans are rare in those areas where the mantle of Kalahari sand is deep.

Where the mantle of Kalahari sand is deep (Figure 2.4) the landscape is made up of undulating sand ridges and swales, one to three metres in height. Large vegetation stabilised sand dunes up to *c.* 20 m in height occur in the

Figure 2.4 Map of the study area showing the approximate extent of the "Kalahari Sand" deposits (shaded) and the "Central Basin" in relation to the main wetland systems in eastern Bushmanland. A = Nyae-Nyae wetland system; B = "Pannetjiesveld" wetland system; C = Klein Dobe wetland system; D = Cin Qo wetland system.


KALAHARI SAND
D
Cin Qo
C
Klein Dobe
CENTRAL BASIN
Tsumkwe
Makuri
Tjokwe
B
Gura
Nyae-Nyae
Gautscha
AHA HILLS
Khabi
A
Kremetartkop
Nama
KALAHARI SAND

north-east of the study area. The Kalahari sands are pervious, deep sands (>1.5 m in depth), showing no horizon development and which are often heavily leached and deficient in soil nutrients (Table 4.1, page 90). As a consequence of the low nutrient status of the soils, forage quality is poor in grasses that occur on Kalahari sands (Cole & Brown, 1976; Cole, 1982; Skarpe, 1986; Skarpe & Bergstrom, 1986).

Most of the surficial expression of the basement geology in eastern Bushmanland occurs in the "Central Basin" area as a result of the combined effects of the Aha Hills obstructing the westward transport of sand and the deflationary effect of the winds during the same period (Ward & Swart, 1989). The "Central Basin" area is largely flat with the Aha Hills in the south-east being the only prominent feature of relief. Micro-relief features such as low calcrete ridges, shallow depressions and drainage lines are the result of the variability of weathering and differential erosion rates of specific geological strata (Cole & Brown, 1976; Hegenberger, 1983).

Soils in the "Central Basin" area are shallow to moderately deep (0.1-1.5 m) and their chemical and physical characteristics vary according to the underlying geological strata and drainage (Table 4.1, page 90). Where drainage is impeded soils show distinct E-horizons and in some cases soils are saline (Table 4.1, page 90).

2.4 CLIMATE

Climatic conditions in eastern Bushmanland are typical of a large part of southern Africa (Tyson, 1986). Shulze & McGee (1978) assign the area a Köppen classification of BShgw; hot, dry steppe with summer rainfall and annual mean temperature above 18 °C.

The climate of the study area is semi-arid. Semi-arid areas are characterised by low annual precipitation, periodic droughts of varying severity and high rates of evaporation. Noy-Meir (1973) defines them as, "those areas with a mean annual rainfall between 200 and 500 mm and where diffuse dryland farming is an unreliable operation". Land-use is limited to the utilisation of the vegetation resources of the area (Walker, 1979a).

As no climatic data, other than rainfall, are available for the study area, the climatic data summarised in Figure 2.5 are for Grootfontein, approximately 280 km West of the study area. Annual wet season (September 1 - August 31) rainfall figures for Tsumkwe are given in Figure 2.6. The data for the 1974/75 and 1975/76 wet seasons are incomplete. These wet seasons were known to have above average rainfall at Grootfontein (Weather Bureau data).

Figure 2.5 Climatogram for Grootfontein (19°36'S 18°08'E).
Key:

- a. Station and altitude (m) above mean sea level
- b. Mean annual temperature (°C)
- c. Mean annual precipitation (mm)
- d. Mean annual precipitation (mm) recorded at Tsumkwe
- e. Highest temperature recorded (°C)
- f. Mean daily maximum temperature of warmest month (°C)
- g. Mean daily minimum temperature of coldest month (°C)
- h. Lowest temperature recorded (°C)

Lined area represents the duration of the wet season.

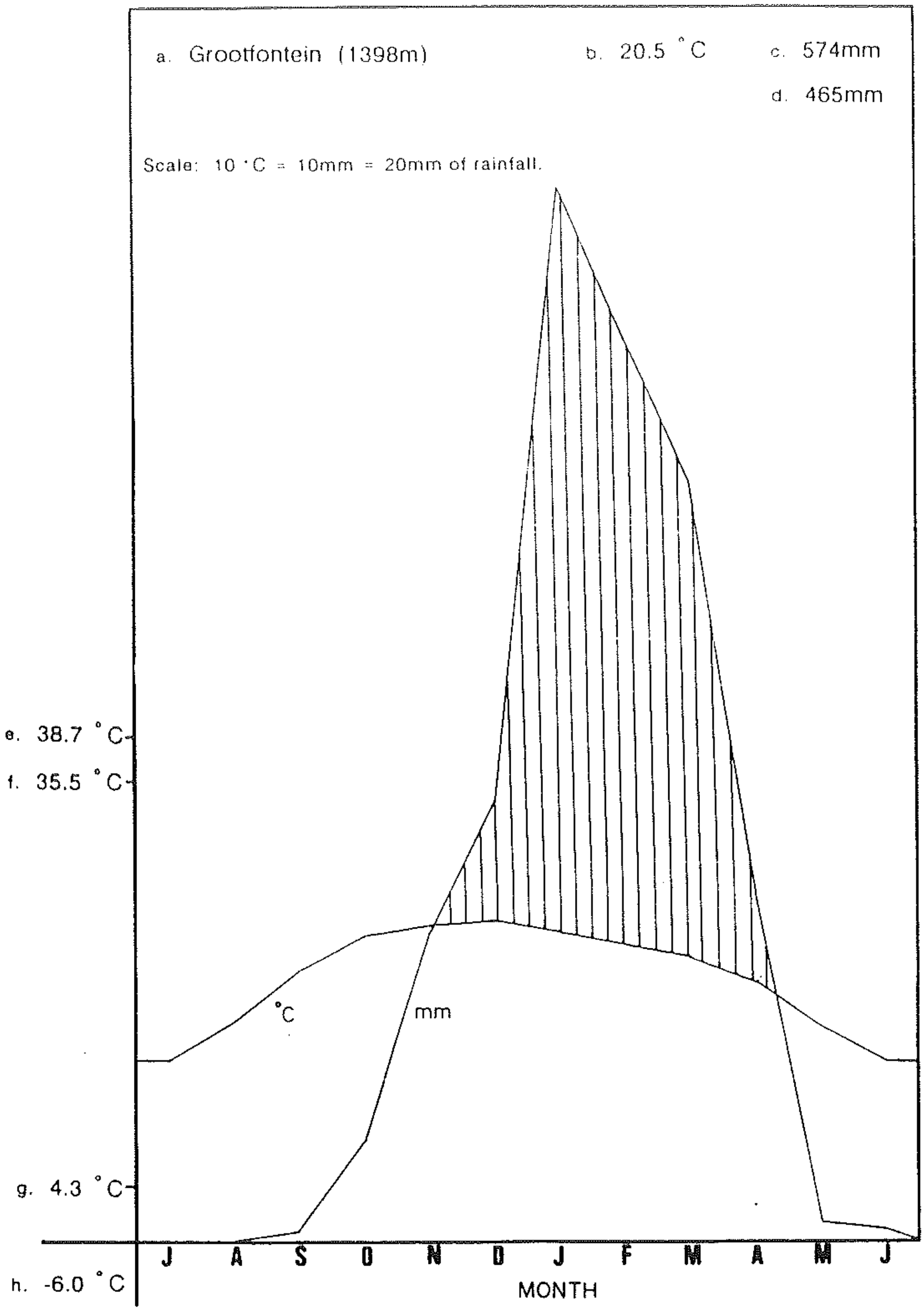
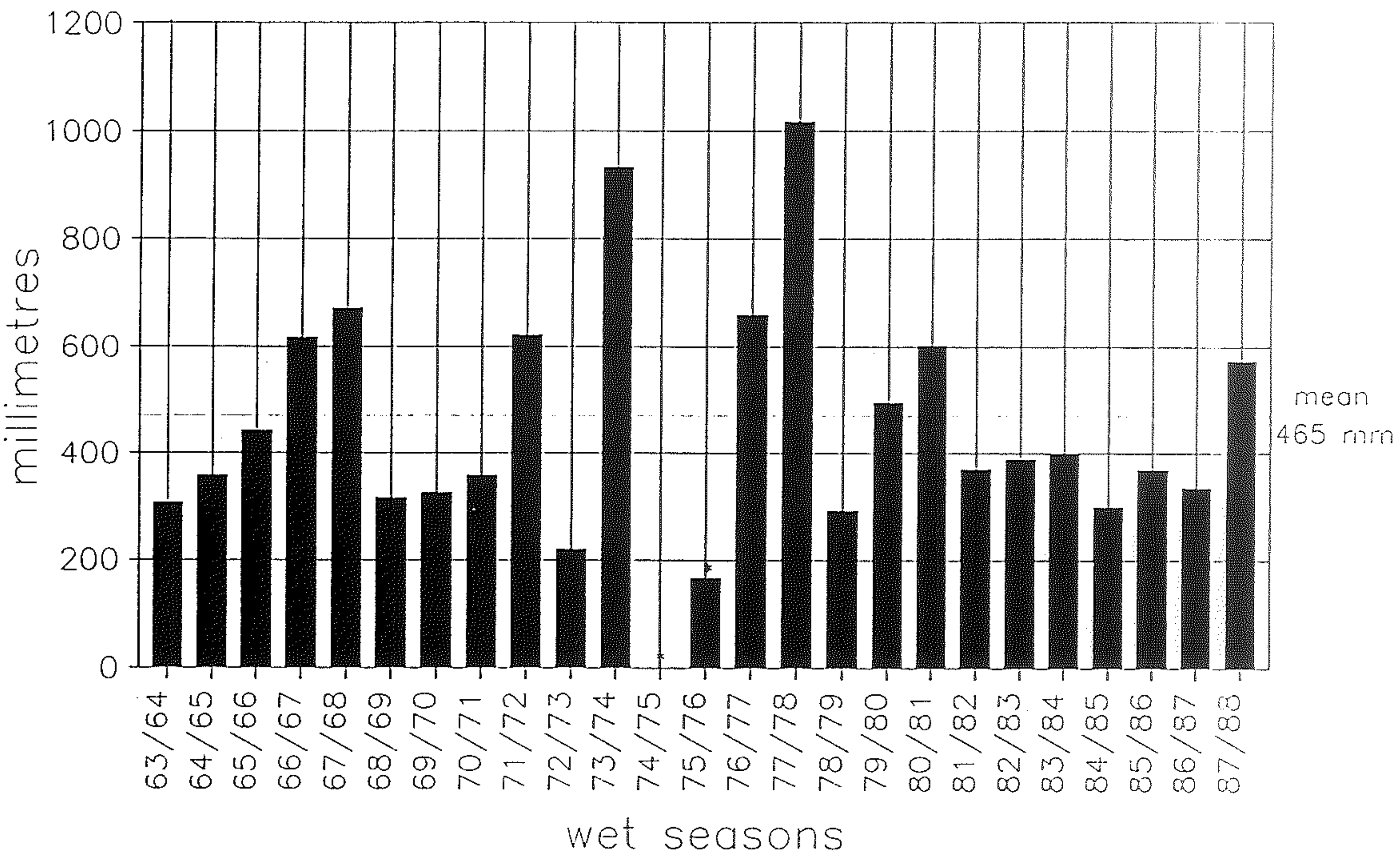

a. Grootfontein (1398m)
b. 20.5 °C
c. 574mm
d. 465mm
Scale: 10 °C = 10mm = 20mm of rainfall.
e. 38.7 °C
f. 35.5 °C
g. 4.3 °C
h. -6.0 °C
°C
mm
J
A
S
O
N
D
J
F
M
A
M
J
MONTH

Figure 2.6 Wet season (September 1 - August 31) rainfall totals for Tsumkwe, Bushmanland. * Data incomplete.


1200
1000
800
600
400
200
0
millimetres
mean
465 mm
63/64
64/65
65/66
66/67
67/68
68/69
69/70
70/71
71/72
72/73
73/74
74/75
75/76
76/77
77/78
78/79
79/80
80/81
81/82
82/83
83/84
84/85
85/86
86/87
87/88
wet seasons

In Figure 2.5 it is clear that rainfall is markedly seasonal over the study area; 90 % of the annual total usually falls between November and April (van der Merwe, 1983). There is a high inter-annual variation in total precipitation (*c.* 25 %; van der Merwe, 1983) as shown in the wet season rainfall totals in Figure 2.6. Winter rainfall is rare, and summer rainfall usually occurs during several discrete storm events. There are usually less than 40 rain days in any one wet season.

Rainfall usually occurs as a discrete seasonal event and superimposed on this is a high level of spatial and temporal variation in rainfall. As rainfall is the factor limiting the rate of plant production in these systems (Rutherford, 1980; McNaughton, 1985; Westoby *et al.*, 1989), the seasonality and variability in rainfall in both space and time has important implications for management and utilisation of the vegetation. As a consequence of the "patchy" nature of rainfall (both within and between years) management systems are complicated as plant production reflects the variability in rainfall. In addition, large tracts of land are required to sustain secondary production of livestock and/or wildlife. The seasonal migrations of wildlife (and people) in semi-arid and arid regions are thought to be a response to the patchiness of the vegetation resources.

The rate of plant growth is not only limited by the low and variable rainfall but by the general aridity as well. Potential evaporative demand (2903 mm per year) exceeds annual precipitation by a factor of five or more (van der Merwe, 1983). This is a result of high temperatures (mean monthly maximum 27 °C), the number of clear days (316 days per year) and the long monthly wind runs (5782 km per month) which reach their peak (6930 km per month) during the end of the dry season in October (Weather Bureau data).

Although frosts are irregularly recorded (once every three to five years (Rushworth, 1975; le Roux *et al.*, 1988)) in other parts of the Kalahari System and have been found to be important determinants of vegetation structure (Rushworth, 1975), no frosts were observed during the course of this study. The presence of frost sensitive species such as *Adansonia digitata* (Coates-Palgrave, 1977) in the study area suggests that the incidence and severity of frost is low.

2.5 A HISTORY OF DEVELOPMENT IN BUSHMANLAND

The area now known as Bushmanland has been occupied by the Ju/'hoan bushmen for centuries. These people practised a hunter-gatherer economy and other than normal trading practices with local bantu tribes, there was little contact with peoples outside of their traditional hunting territory known as Nyae-Nyae until the late 1950's (Marshall, 1976).

In 1959 the first formal administrative centre was established at Tsumkwe, and development in the area was restricted to low intensity projects (fence dropper cutting, small stock husbandry and gardens) that soon became overwhelmed by the numbers of people settling at Tsumkwe (van Rooyen, 1991). Development remained largely static until 1970 when Bushmanland was formally established "as a homeland for people classified as Bushmen", on the recommendations of the 1963 Odendaal Commission (Anon., 1964). In accordance with the recommendations of the Odendaal Commission money was spent on developing Bushmanland and there was a rapid build up of infrastructure (Jones, 1991).

A consequence of the proclamation of Bushmanland was that the Ju/'hoansi were suddenly restricted to about 35 % of their original hunting area (Marshall & Ritchie, 1982). The population became centred on Tsumkwe, which rapidly turned into a rural slum, and local game and bushfood resources were quickly depleted. Little wage labour was available, and the Ju/'hoansi became increasingly dependant on welfare from government departments. Through the 1970's and 1980's the military situation in northern Namibia gave rise to an increasing number of jobs in the army for young men. This led to an almost total dependence on an economy based on military wages in Bushmanland, with few people practising their traditional hunting and gathering lifestyle (Marshall & Hartung, 1986). The disbanding of the South West African army on Independence saw the collapse of this cash economy, and an increasing dependence of certain sectors of the local communities on government controlled welfare programmes.

Starting in the early 1980's the Ju/'hoansi were encouraged by the then Ju/Wa Development Foundation (now the Ju/'hoan Bushman Development Foundation) to leave the "urban" settlement of Tsumkwe and start developing a subsistence livestock industry, supplemented by planted gardens and hunting and gathering (Adams *et al.*, 1990). This non-governmental organisation (NGO) provided inputs of cattle, boreholes and advice. This decentralisation of the population was a response to:

a) the perceived threat of land dispossession through the proclamation of a National Park in eastern Bushmanland, which involved resettlement of people outside the proposed National Park boundaries and strict limits on activities of the local people within the Park boundaries, and;

b) a genuine desire to develop a broader economy than one founded on welfare aid and hunter-gathering practices (Biesele, 1991).

The programme of decentralised settlements in eastern Bushmanland led to the establishment of villages at waterholes originally developed for wildlife, and a situation of conflict arose between the people of these settlements and the authorities controlling wildlife resources (then the Department of Nature Conservation and Tourism). This ultimately led to a dichotomous view of development in the area, with one group advocating a wildlife-or-nothing scenario and the other group espousing a livestock development option. There was little consultation between these opposing factions and the true values of the wildlife resources were lost in a situation of distrust and conflict.

Recent developments initiated by the Ministry of Wildlife and local NGO's has led to a consultative process in which much common ground has been found (Jones, 1991). The recognition by the Ministry of Wildlife that the people of the area have real and inviolate rights to the land and the resources, has brought about a greater understanding of the aspirations of the Ju/'hoansi and their desire to develop the wildlife resources of the area. Since the inception of the decentralised village programme questions have been raised as to the economics of a subsistence livestock industry as sole provider of an economic base for these communities. There is now recognition by the NGO's in Bushmanland that there is an urgent need to develop a productive and viable economic enterprise in which the Ju/'hoansi can play a meaningful role (Cumming, 1989) and that this may have to be based on the wildlife resources of the area (van Rooyen, 1991).

2.6 CONCLUSION

The harsh and variable climatic conditions prevailing in eastern Bushmanland precludes the development of dryland cropping as the basis for a sustainable local economy. The only viable development option at present is the use of the indigenous vegetation resources of the area for the secondary production of either domestic livestock or wildlife.

The management of these resources is, however, likely to be complex as the vegetation comprises a heterogeneous mosaic determined largely by the influence of the fragmented basement geology on the soils of the area. Superimposed onto this mosaic, the temporal and spatial variability of rainfall is likely to further complicate the management inputs required to promote sustainabilty, as plant production is not only affected by species composition of individual vegetation units but by the dispersal and timing of rainfall as well.

The species composition, distribution and structure of the vegetation units (termed associations in this study), their determinants and the importance of these determinants on the development and management of the area are the subject of the following chapters.

CHAPTER THREE

THE PHYTOSOCIOLOGY OF EASTERN BUSHMANLAND - SPECIES COMPOSITION, STRUCTURE AND PHYTOCHOROLOGY OF THE VEGETATION ASSOCIATIONS

3.1 INTRODUCTION

The Kalahari System south of the Okavango River is often referred to as the "Kalahari Desert", because it is characterised by a lack of perennial surface water, seasonal droughts and high summer temperatures. The lack of reliable sources of water proved to be a major barrier to the exploration of this region during the early years of European settlement and expansion in southern Africa and the Kalahari Desert remained largely uninhabited by Europeans until the early 1900's (Main, 1987).

The botanical exploration of the Kalahari Desert is reviewed by Leistner (1967). Most of the early work in the region was taxonomic and based on few collections. As a result descriptions of the vegetation were superficial (e.g. Pole-Evans, 1936), and it was not until after the

Second World War that the state of botanical knowledge of the region improved notably. The botany and ecology of the region is still not well understood.

Maps depicting broad vegetation types have been produced by Volk (1965), Wild & Barbosa (1967), Weare & Yalala (1971), Giess (1971) and more recently by several consulting agencies (e.g. van Gils, 1986). These studies are mainly physiognomic and are floristically incomplete.

Comprehensive phytosociological data are only available from the southernmost Kalahari. Leistner (1967) described the vegetation of the Kalahari Gemsbok Park in detail, and Skarpe (1986) used this study as the basis of her later work on the vegetation of south-western Botswana. The geobotanical studies of Cole and co-workers (Cole & Brown, 1976; Cole & le Roux, 1978; Cole, 1982; Cole, 1986) provide useful botanical information but provide little floristic detail. These studies addressed specific aspects of the southern Kalahari system with widely divergent objectives. As a consequence a thorough analysis of the phytosociology and phytogeography of the Kalahari region is not yet available (Skarpe, 1986), and the chorological position of vegetation of the Kalahari System south of the Okavango River is still under debate (Volk, 1965; Werger, 1978; White, 1965, 1971 & 1983).

This chapter contributes to both a local and a broader knowledge of the phytosociology of the Kalahari System. The phytosociology (composition, structure and distribution) of the vegetation associations identified in the study area is described and the distribution of the associations elsewhere in the Kalahari System and southern Africa, is reviewed. The phytochorological position of the study area is analyzed with reference to postulated phytochorological boundaries.

The conservation value and conservation priority of the study area at both a local (Namibian) and regional level (southern Africa) is discussed with reference to the International Union for the Conservation of Nature and Natural Resources (IUCN) concepts of uniqueness and diversity (IUCN, 1980).

3.2 METHODS

3.2.1 *Survey methods.*

A large number of sampling techniques are available for use in phytosociological studies, and each has its advantages and disadvantages. In this study, floristic and environmental data were collected using the Braun-Blanquet approach to phytosociology (Mueller-Dombois & Ellenberg, 1974; Werger, 1974). This approach was selected for several reasons. It has been shown to have a wide application in a variety of vegetation types in southern Africa (Leistner & Werger, 1973; Bredenkamp & Theron, 1985; McDonald, 1987; le Roux *et al.* 1988; Lubke & Strong, 1988); the technique is simple, easily learned and the observer becomes increasingly proficient with time; it is replicable and cost efficient; several statistical packages are available for the analysis of the data and the output is easily interpreted.

Data were collected from 224 sample sites determined using the random-stratified method described by Craig (1983). Sample plots (quadrats) were distributed to include as much variation in the study area as possible and to be representative of homogenous stands of vegetation.

Quadrat sizes varied according to vegetation type (Table 3.1) and were derived from species-area curves (Rice & Kelting 1955; Greig-Smith, 1983) determined during the preliminary stages of the study. Large quadrat sizes (20 m x 20 m) were required to adequately sample woodland vegetation. However, such large sample plots are not required for herbaceous and shrub vegetation. Where a single species of grass dominated the herb layer a 2 m x 2 m sample plot was adequate (for example the *Odyssea paucinervis* grasslands; referred to as single dominant species grasslands in Table 3.1).

Table 3.1 Generalised vegetation types and sample plot sizes used in this study.

VEGETATION TYPE	SAMPLE PLOT SIZE
Single dominant species grasslands	2m x 2m
Multispecies grasslands	5m x 5m
Shrub/Scrubland	10m x 20m
Woodland	20m x 20m

Cover-abundance values were assigned to all plant species recorded within the quadrat according to the scale given by Werger (1974), (Table 3.2).

Table 3.2 Cover-abundance values assigned and the percentage cover of the values used in this study.

VALUE	PERCENTAGE COVER
+	less than 1% of total plot area
1	1 - 5% of total plot area
2a	5 - 12% of total plot area
2b	13 - 25% of total plot area
3	26 - 50% of total plot area
4	51 - 75% of total plot area
5	76 - 100% of total plot area

Structural data were also collected at each sample site.

In this study the tree layer is defined as comprising those woody species >3 m in height, the shrub layer as comprising all woody species <3 m in height and the herbaceous layer as being made up largely of non-woody herbs and grasses <1.5 m in height.

Site related data recorded included: geomorphological unit, slope, underlying geological formation, soil depth (depth to hardpan layer or rock), soil colour, soil form (MacVicar *et al.* 1977), and geographical location. Cover of surface rocks and litter were estimated on a percentage scale at each sample site.

All plant specimens collected are lodged with the National Herbarium, Windhoek. Identifications were confirmed by the Herbarium and nomenclature follows Merxmuller (1966-72) and Gibbs Russell *et al.* (1985, 1987 & 1990). All species recorded during the study are listed in Appendix 1.

3.2.2 *Data analysis.*

3.2.2.1 Classification of floristic data.

Cover-abundance data from the sample sites were classified using two-way indicator species analysis (TWINSPAN: Hill 1979a). TWINSPAN was used in this study as it has been shown to be robust in its handling of large data sets (Gauch, 1982), it is regarded as state of the art in numerical classification (Kent & Ballard, 1988) and can be used on micro-computers. As TWINSPAN cannot accept Braun-Blanquet cover-abundance values directly for analysis these were transformed using the following series: + = 1, 1 = 2, 2a = 3, 2b = 4, 3 = 5, 4 = 6, 5 = 7 (Lubke & Strong, 1988).

The clusters produced by TWINSPAN are described as associations *sensu* Mueller-Dombois & Ellenberg (1974) - "of definite floristic composition, uniform physiognomy and uniform habitat conditions".

Species fidelity is a fundamental concept of the Braun-Blanquet approach to phytosociology and is defined by Barkman (1989) as, "the degree of preference of a species for a given association". If a species has an optimum in one syntaxon only it is a *character* species; if it has several phytosociological optima, it is a *differential* species (Barkman, 1989). Character and differential species form the *diagnostic* species in contrast to *companion* species that are more or equally frequent in other syntaxa. The constant companion species and the diagnostic species form the *characteristic* species combination of a syntaxon (Barkman, 1989).

In this study associations are named according to differential species and described using characteristic species. The structural description in the name of the association follows the structural classification proposed by Edwards (1983).

The synoptic frequencies given in Tables 3.3, 3.4, and 3.5 (pages 38, 49 & 63 respectively) were determined using the following scale (Greig-Smith, 1983):

I - species occurs in 1-20% of the associations.
II - " " " 21-40% " " "
III - " " " 41-60% " " "
IV - " " " 61-80% " " "
V - " " " 81-100% " " "

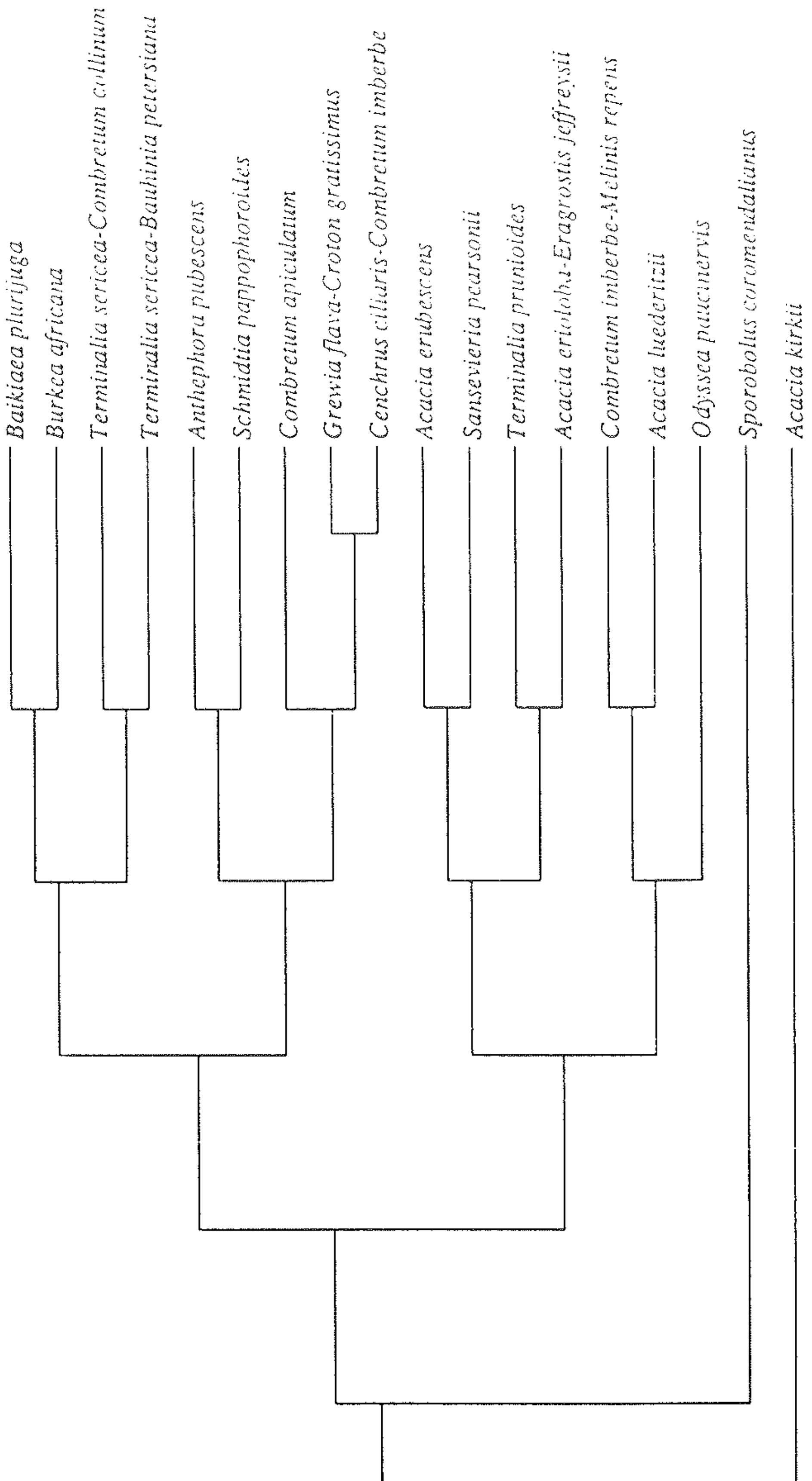
Species occurring fewer than three times in the data set were removed before analysis as they tended to create "noise" in the analysis (Gauch, 1982) and obscured some of the cluster groupings.

3.3 RESULTS

Eighteen vegetation associations were identified in eastern Bushmanland (Figure 3.1). These associations can be floristically divided into three groups:

(i) Associations restricted to shallow soils and/or temporarily flooded habitats in the "Central Basin"

Figure 3.1 TWINSPAN dendrogram of the classification of the floristic data.


Baikiaea plurijuga
Burkea africana
Terminalia sericea-Combretum collinum
Terminalia sericea-Bauhinia petersiana
Anthephora pubescens
Schmidtia pappophoroides
Combretum apiculatum
Grewia flava-Croton gratissimus
Cenchrus ciliaris-Combretum imberbe
Acacia erubescens
Sansevieria pearsonii
Terminalia prunioides
Acacia erioloba-Eragrostis jeffreysii
Combretum imberbe-Melinis repens
Acacia luederitzii
Odyssea paucinervis
Sporobolus coromendalianus
Acacia kirkii

area (Associations A to F and K);

(ii) Associations occupying moderately deep soils transitional between the "Central Basin" and the deep "Kalahari Sand" areas (Associations G to J, and L to N);

(iii) Associations restricted to the deep "Kalahari Sand" deposits (Associations O to R).

As tables generated by TWINSPAN are bulky and difficult to read and interpret directly, the "raw" TWINSPAN table has been divided into three smaller tables. The synoptic frequencies of the characteristic species in each of the identified associations are given in Tables 3.3 (page 38), 3.4 (page 49) and 3.5 (page 63). A species had to be diagnostic with regard to its presence in an association to be included in the synoptic tables.

The floristic composition, structure and distribution within the study area, of each of the associations is described below.

3.3.1 *Description of the vegetation associations.*

A. *Acacia kirkii - Echinochloa colona* wetland association (Table 3.3, page 38).

This association is characterised by stands of evenly spaced (*c.* two to three metres apart), individual trees of

Acacia kirkii. These trees are usually four to six metres in height and form a distinct zone around the wetland margin (Plate 3.1).

Plate 3.1. *Acacia kirkii* - *Echinochloa colona* wetland association. *Acacia kirkii* forms a distinct zone along the wetland margin. *Echinochloa colona* and *Oryzidium barnardii* are the dominant grasses.

The herbaceous layer along the margin is dominated by hygrophilous grasses and sedges up to one metre high. *Echinochloa colona* forms dense cover of up to 60 %. Other common species of grass are *Echinochloa stagnina, Oryzidium barnardii* and *Eragrostis rotifer*. Sedges are common and widespread, but nowhere do they contribute more than 5 % of the total cover. Characteristic species are *Cyperus sphaerospermus, Schoenoplectus muricinux* and

Table 3.3 Synoptic frequencies of the characteristic species occurring in Associations A-F. Association groupings generated by TWINSPAN. Key to associations: A = *Acacia kirkii* wetland; B = *Odyssea paucinervis* grassland; C = *Acacia luederitzii* - *Combretum hereroense* woodland; D = *Combretum imberbe* - *Melinis repens* woodland; E = *Sprobolus coromendalianus* grassland; F = *Sansevieria pearsonii* - *Croton menyhardtii* thicket.

SPECIES	ASSOCIATION					
	A	B	C	D	E	F
No. of releves	6	6	8	5	7	8
Total No. of species	33	20	49	38	22	63
Acacia kirkii	V					
Nymphaea capensis	V					
Eleocharis limosa	V					
Aponogeton desertorum	V					
Echinochloa colona	V					
Nymphoides indica	IV					
Sporobolus coromendalianus					V	
Hermannia linearis					V	
Portulaca hereroensis					V	
Trianthema triquetra		V			III	
Sporobolus spicatus		IV				
Sporobolus ioclados		III				
Odyssea paucinervis		V	V			
Eragrostis echinochloidea		IV	III			
Acacia luederitzii			V			
Heliotropium ovalifolium			V			
Anthephora schinzii			V			
Combretum hereroense			V			
Maytenus senegalensis			III			
Pergularia daemia			IV			
Enneapogon cenchroides		III	V	V		
Sericorema sericea			V	V		
Aristida adscensionis			IV	V		
Combretum imberbe			IV	V		
Melinis repens			V	V		
Commelina forskalaei			III	IV		IV
Urochloa brachyura				IV		IV
Aristida rhiniochloa				V		
Eragrostis rigidior				III		
Ziziphus mucronata				III		
Acacia erubescens						V
Croton menyhartii						V
Sansevieria pearsonii						V
Chloris virgata						IV
Brachiaria deflexa						III
Pupalia lappacea						III
Panicum maximum						IV
Terminalia prunioides						V
Commiphora africana						IV
Commiphora pyrocanthoides						V
Dichrostachys cinerea						V

Schoenoplectus praelongatus. Several small aquatic forbs are common in the littoral zone of these wetlands. These include *Nymphoides indica, Aponogeton desertorum, Craterostigma plantagineum* and the fern *Marsilea unicornis*. Where the water depth exceeds *c*.0.4 m, *Nymphaea capensis* is the dominant floating-leaved macrophyte. *Polygonum limbatum, Ottelia kuneniensis* and *Eleocharis limosa* are also common.

This association is restricted in its distribution to the granitic extrusion in central Bushmanland (Figure 2.4, page 15). It is established where shallow, periodically flooded depressions have formed on the joints and fractures in the granite (see Plate 2.1, page 13). The soils are organic clays which may show vertic (self-mulching) characteristics.

B. *Odyssea paucinervis* closed grassland association (Table 3.3, page 38).

Trees and shrubs are absent from this association. The herbaceous layer is dominated by the short (<0.4 m) grass *Odyssea paucinervis* (Plate 3.2), with cover values usually in excess of 50 %, but seldom exceeding 75 %. Other characteristic grass species are *Sporobolus spicatus, Sporobolus iocladus* and *Eragrostis echinochloidea* which occur at cover values of less than 5 %.

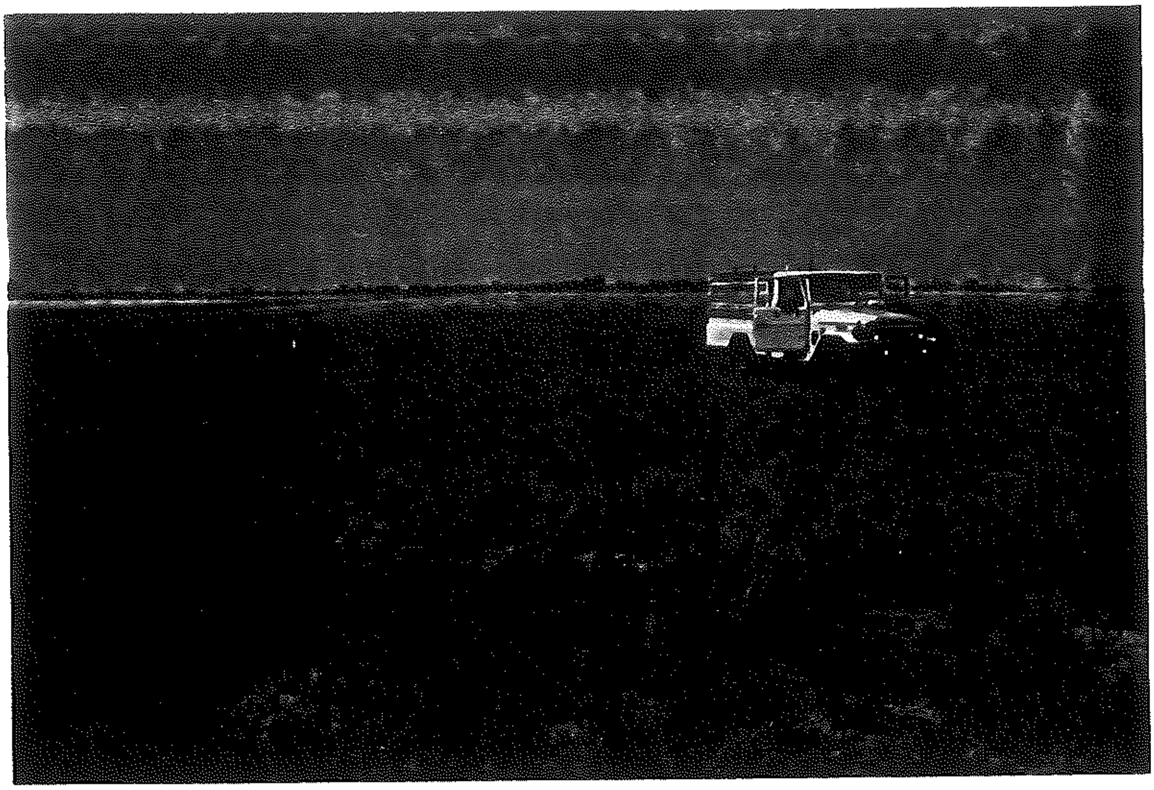


Plate 3.2. *Odyssea paucinervis* association. *Odyssea paucinervis* forming dense, almost mono-specific stands on a lunette dune on the western margin of Khabi Pan.

Common forbs in the association include *Leucosphaera bainesii, Petalidium variabile, Heliotropium ovalifolium, Trianthema triquetra* and *Gisekia africana.*

This association is restricted in its distribution to the calcareous sand accumulations and lunette dunes around the larger pans particularly in the Nyae-Nyae area, south of Tsumkwe. These sands have high sodium levels (>200 μmol.gm^{-1}), high calcium levels and high pH (7.8-9.0) (Table 4.1, page 90).

C. *Acacia luederitzii - Combretum hereroense* short, open woodland association (Table 3.3, page 38).

The woody component of the association is dominated by *Acacia luederitzii, Combretum hereroense* and *Combretum imberbe* (Plate 3.3). All these species rarely exceed five metres in height and occur at cover values of less than 10 %. Other common trees and shrubs are *Acacia mellifera, Mundulea sericea, Rhus tenuinervis, Maytenus senegalensis* and *Ipomoea adenioides.*

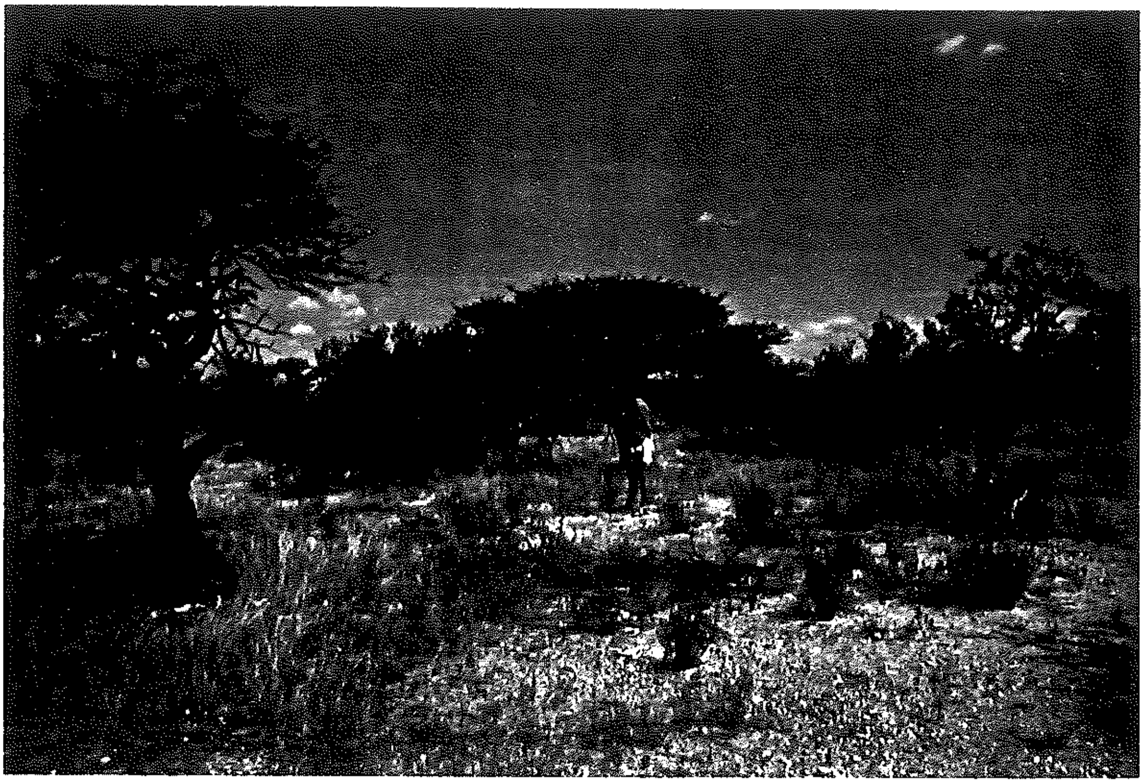


Plate 3.3. *Acacia luederitzii - Combretum hereroense* association. *Acacia luederitzii* (left foreground) and *C. hereroense* (right) dominate the tree layer. Note sparse ground cover.

The herbaceous layer is characterised by few species at low cover values (1-<5 %). Where pockets of calcareous sand occur *Odyssea paucinervis* and *Enneapogon cenchroides* are the dominant grasses. *Melinis repens, Diplachne fusca* and *Panicum gilvum* are the dominant grasses in those areas subject to flooding during the wet season. A number of forbs are characteristic of this association. These include the creeper *Pergularia daemia*, and the annuals *Sericorema sericea, Phyllanthus pentandrus, Heliotropium ovalifolium* and several species of *Commelina*.

The distribution of the association is restricted to the central Nyae-Nyae pan system (Figure 2.4, page 15) where it is found on shallow (<0.2 m) litholitic soils surrounding the main pans in the area (Table 4.1, page 90). The soils are underlain by a pedogenic hardpan calcrete and drainage is poor.

D. *Combretum imberbe - Melinis repens* tall, open woodland association (Table 3.3, page 38).

Combretum imberbe is the only tree species found in this association and is typically eight to twelve metres in height, with cover values ranging from 5-12 % (Plate 3.4). Shrub forms of *Ziziphus mucronata* and *Acacia luederitzii* may be found on elevated sites. The herbaceous layer is dominated by annual grasses, principally *Melinis repens,* which often grows in dense monospecific stands with cover values of up to 65 %. Other common grass species are *Aristida rhiniochloa, Aristida adscensionis, Eragrostis rotifer* and *Setaria verticilata* which occupies the shady areas below trees and shrubs.

Plate 3.4. *Combretum imberbe - Melinis repens* association. *Combretum imberbe* is the only tree species present. The herbaceous layer is dominated by *M. repens*. *Eragrostis rotifer* (tall grass on right) is characteristic of wetter sites.

Few forbs occur in this association, usually with cover values of 1 % or less. *Sericorema sericea* is the only species with a high constancy. Other forbs include *Polygonum limbatum, Sesbania macowanii* and *Commelina forskalaei*.

This association is characteristic of shallow depressions subject to prolonged flooding (one to two months), and forms a mosaic with the *Acacia luederitzii* - *Combretum hereroense* association in the Nyae-Nyae pans area. Soils are shallow (<0.15 m) and overlie pedogenic hardpan calcrete (Table 4.1, page 90).

E. *Sporobolus coromendalianus* open grassland association (Table 3.3, page 38).

No woody plant species occur in this association (Plate 3.5). The grass *Sporobolus coromendalianus* is the only species with cover values higher than 5 % and is differential for the association. Geophytes such as *Eriospermum bakeranum* and *Nerine laticoma* are common. Other forbs characteristic of this association are *Hermstaedtia linearis, Ipomoea coptica* and the succulents *Portulaca hereroensis* and *Trianthema triquetra*. In certain areas individual specimens of *Ipomoea adenioides* up to 1.2 m tall are characteristic.

This association is of limited extent and is found in areas where drainage has been impeded by an impervious layer of clay. Soils are shallow (<0.3 m) above the clay layer, have high sodium values (>400 μmol.gm^{-1}) (Table 4.1, page 90) and have a characteristic, leached E-horizon just above the clay layer. In the Klein Dobe area a layer of hard plinthite replaces the clay layer.

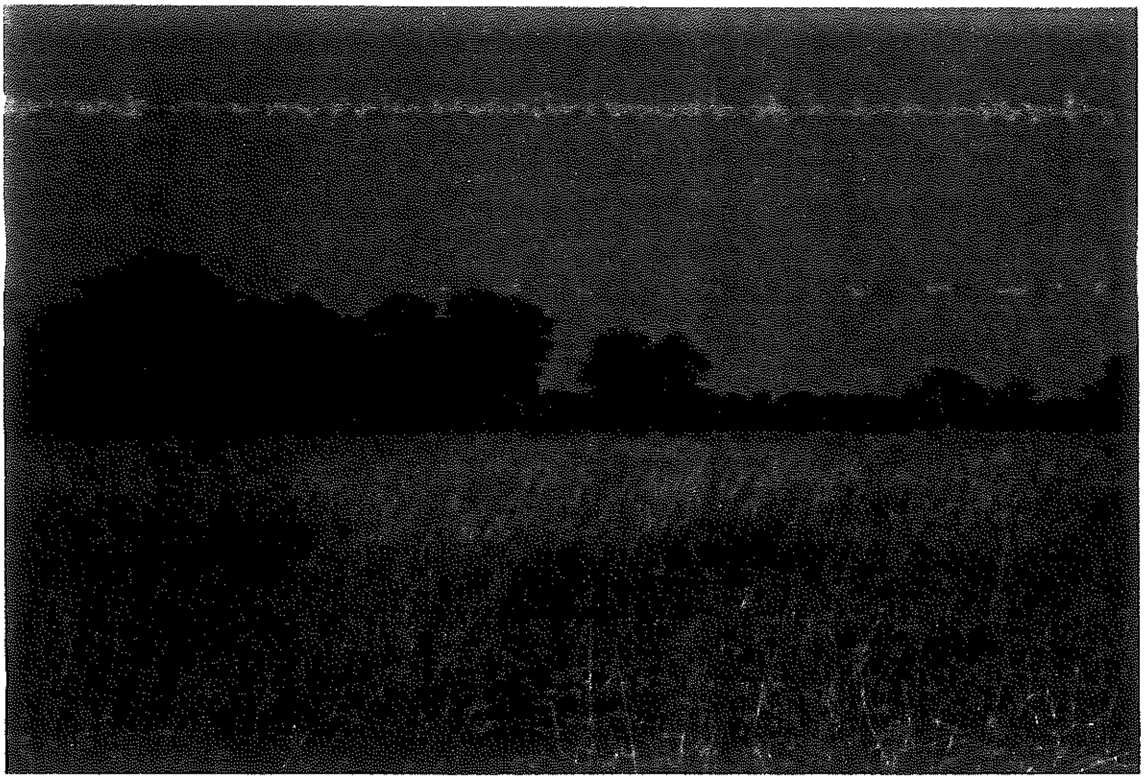


Plate 3.5. *Sporobolus coromendalianus* association. *Sporobolus coromendalianus* dominates the ground layer. Note the absence of woody species. The woody habitat in the background is a *Sansevieria pearsonii* - *Croton menyhartii* thicket.

F. *Sansevieria pearsonii* - *Croton menyhartii* thicket association (Table 3.3, page 38).

This association typically has a tree layer (10-20 % cover) dominated by *Terminalia prunioides* and *Acacia erubescens* (Plate 3.6). Other tree species common in this association are *Acacia tortilis, Albizia anthelmintica, Albizia harveyii, Spirostachys africana* and *Cassine transvaalense*. The multistemmed shrub *Croton menyhartii* is differential for this association.

Plate 3.6. *Sansevieria pearsonii - Croton menyhartii* association. *Sansevieria pearsonii* dominates the herbaceous layer. Woody species include, *Acacia erubescens* (left foreground), *Terminalia prunioides* (tallest species) and *C. menyhartii* (shrubs on right, near person).

The herbaceous layer is dominated by *Sansevieria pearsonii,* which can form dense stands of between 50 % and 85 % cover. Grasses such as *Panicum maximum, Urochloa brachyura* and *Aristida rhiniochloa* are found along the margins of the *Sansevieria pearsonii* stands, usually at cover values of less than 1 %. Succulent forbs are found within the *Sansevieria pearsonii* stands. These include *Huernia verreckeri, Caruluma lugardae, Duvalia polita* and several *Ceropegia* species.

This association forms a mosaic with the *Sporobolus coromendalianus* association (E) (Plate 3.5), occupying slightly elevated sites not subject to flooding. Soils are deeper (>0.5 m) and have lower sodium values ($<200\ \mu mol.gm^{-1}$) than at the *Sporobolus coromendalianus* (E) sites (Table 4.1, page 90). A clearly defined E-horizon is present in the soil.

G. *Terminalia prunioides* tall, closed woodland and thicket association (Table 3.4, page 49).

Terminalia prunioides dominates the tree layer of this association, forming almost mono-specific stands in which other tree species are rare (Plate 3.7). Trees are usually between six and twelve metres in height and cover values range from 45 % to 80 %. Several species of woody understorey shrubs are characteristic. These include *Croton grattisimus, Grewia flava, Grewia bicolor, Commiphora africana* and *Ximenia americana*. Where grasses provide high cover (*c.* 20 %) in the herbaceous layer, forbs tend to be rare, and *vice-versa*. Total cover provided by grass and forbs rarely exceeds 25 %. There is often a dense layer of leaflitter which may suppress plant growth. *Panicum maximum* is the dominant grass species in this association, but annuals such as *Urochloa brachyura* and *Brachiaria deflexa* are present at most sites. Where forbs dominate the herbaceous layer the dominant species are *Pupalia lappacea, Achyranthes sicula* and *Barleria* *sinensis.*

Plate 3.7. *Terminalia prunioides* association. *Terminalia prunioides* is the dominant tree species often to the exclusion of other species. *Panicum maximum* is the dominant grass species.

This association forms discrete units with well defined boundaries throughout the study area and is highly variable in extent (1-100 ha). Soils are deep (>1.5 m), fine grained sands (Table 4.1, page 90). The distribution of this association shows a close correlation with certain features of subsurface geology. This aspect is well illustrated in the north of the study area, where the *Terminalia prunioides* thickets closely follow the fold structures in the underlying geological strata (Plate 2.2, page 13).

Table 3.4 Synoptic frequencies of the characteristic species occurring in Associations G-L. Association groupings generated by TWINSPAN. Key to associations: G = *Terminalia pruniodes* woodland; H = *Acacia erubescens* woodland; I = *Acacia erioloba* - *Eragrostis jeffreysii* woodland; J = *Cenchrus ciliaris* - *Combretum imberbe* woodland; K = *Grewia flava* - *Croton grattisimus* shrubland; L = *Combretum apiculatum* woodland.

SPECIES	ASSOCIATION					
	G	H	I	J	K	L
No. of releves	16	8	7	5	17	26
Total No. of species	75	74	74	50	91	114
Terminalia prunioides	V					
Pupalia lappacea	V					
Barleria senensis	III					
Brachiaria deflexa	IV					
Achyranthes sicula	IV					
Panicum maximum	IV					II
Commiphora africana	V					IV
Croton gratissimus	V	IV			IV	IV
Grewia flavescens	IV	III	IV			II
Acacia erubescens		V				
Brachiaria nigripedata		III				
Eragrostis nindensis		V				III
Commiphora pyrocanthoides	III	V		IV	IV	IV
Lonchocarpus nelsii			V			
Acacia erioloba			V			
Boscia albitrunca			V	III		
Mundulea sericea	II		IV			
Eragrostis lehmanniana			III			
Eragrostis jeffreysii			III			
Rhus marlothii	II		V	V		
Combretum imberbe		III		V		
Aristida meriodionalis				III		
Melinis repens				III	II	IV
Dichrostachys cinerea	IV		IV		IV	IV
Urochloa brachyura	III	V	III	III	III	IV
Digitaria eriantha		V	IV	V	IV	IV
Grewia bicolor		V	IV	III	V	IV
Schmidtia pappophoroides		III	III	IV	III	IV
Combretum hereroense		III	IV	V	IV	II
Grewia flava		IV	V	V	V	III
Eragrostis rigidior			IV	III	III	II
Acacia mellifera	III		IV		III	
Ziziphus mucronata				IV	III	
Cenchrus ciliaris				V	IV	
Maytenus senegalensis				V		IV
Enneapogon scoparius				V	III	
Acacia luederitzii					III	
Catophractes alexandrii					III	
Cyperus margaritaceus					III	
Eragrostis echinochloidea					III	
Ozoroa paniculosa					III	
Vigna decipiens					III	
Stipagrostis uniplumis				V	V	III
Aristida rhiniochloa		III			IV	V
Aristida adscensionis					II	V
Combretum apiculatum	III					V
Acacia fleckii	III					V
Commelina forskalaei		III				III
Neorautanenia mitis						IV
Sclerocarya birrea						III
Eragrostis dinteri						V

H. *Acacia erubescens* tall, open woodland association (Table 3.4, page 49).

Acacia erubescens is the characteristic tree species in this association, usually with cover values less than 12 % (Plate 3.8). Other tree species typical of this association are *Terminalia prunioides* and *Combretum imberbe*. Woody shrubs are common and include *Croton grattisimus, Grewia flava, Grewia flavescens, Grewia bicolor* and *Commiphora pyracanthoides*.

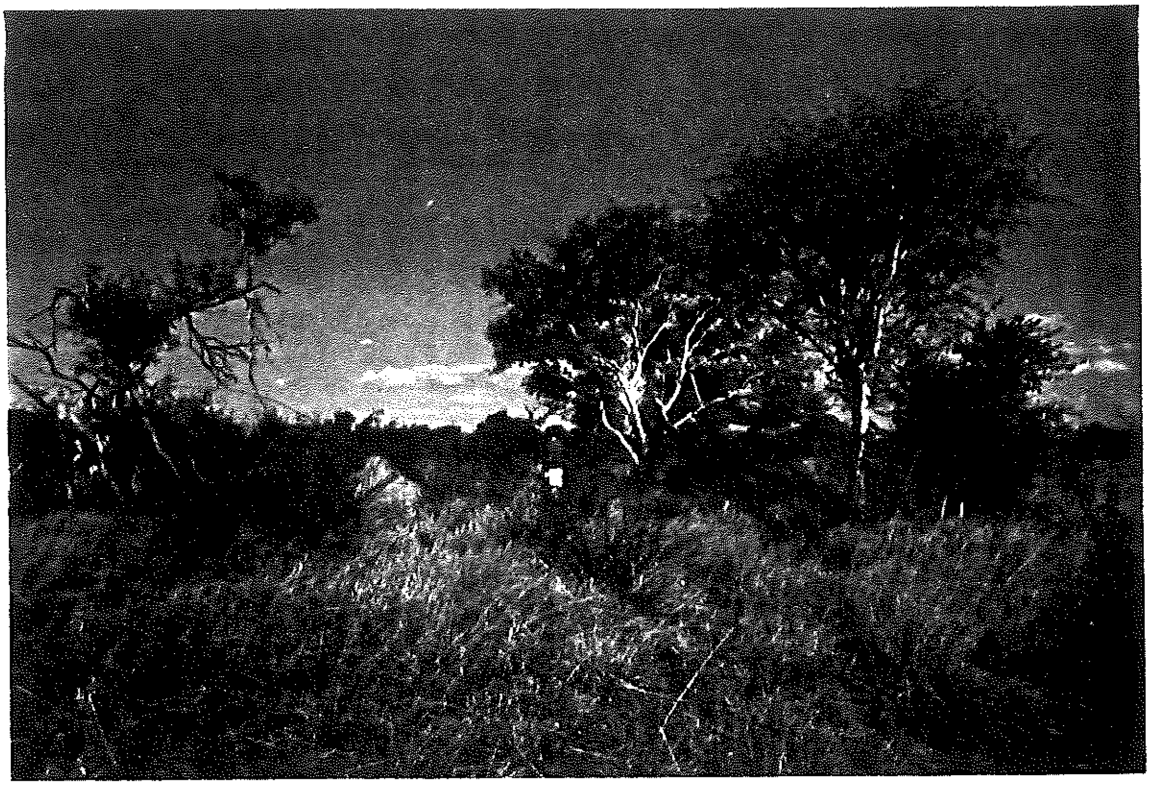


Plate 3.8. *Acacia erubescens* association. *Acacia erubescens* is the most characteristic tree species, with *C. imberbe* (extreme right) often present. Shrubs include several *Grewia* spp. which are usually associated with termitaria.

The herbaceous layer is characterised by a sparse cover (1-5 %) of annual grasses such as *Aristida rhiniochloa, Aristida adscensionis, Urochloa brachyura* and *Eragrostis superba*. Where standing water occurs as a result of impeded drainage *Aristida hordeacea* forms dense stands (*c.* 20 % cover). The perennials *Schmidtia pappophoroides, Eragrostis rigidior* and *Digitaria eriantha* can provide up to 12 % cover at well drained sites. Forbs provide very little cover (<1 %) and few species occur in this association.

Extensive stands of this association are found along the fringes of the *Sporobolus coromendalianus* (E) and *Sansevieria pearsonii - Croton menyhartii* (F) associations to the north and east of Tsumkwe. Soils are sandy loams which vary in depth (0.4->1.5 m) (Table 4.1, page 90) and can have an impervious clay layer below a weakly developed E-horizon.

I. *Acacia erioloba - Eragrostis jeffreysii* tall, closed woodland association (Table 3.4, page 49).

The woody component of this association is clearly stratified. *Acacia erioloba* dominates the tree layer above ten metres, with *Lonchocarpus nelsii, Combretum psidioides* and *Boscia albitrunca* forming a distinct stratum below four metres (Plate 3.9). The shrub layer is characterised by *Combretum hereroense, Dichrostachys* *cinerea, Grewia flava, Rhus marlothii* and *Commiphora africana*. Perennial grasses including *Schmidtia pappophoroides, Digitaria eriantha* and *Eragrostis rigidior* dominate the herbaceous layer. *Eragrostis jeffreysii* is differential for the association at low cover values (1-5 %).

Plate 3.9. *Acacia erioloba - Eragrostis jeffreysii* association. *Acacia erioloba* (left) is the dominant large tree species. *Acacia mellifera* (right), *Lonchocarpus nelsii* (left background, centre) and *Grewia* spp. (right foreground) are also characteristic of this association.

Forbs are well represented and include geophytes such as *Albuca amboensis* and *Eulophia speciosa*. Characteristic annuals include *Hemizygia bracteosa, Talinum arnotti* and *Gisekia africana*.

This association is found distributed in a broad north-south orientated belt along the western margin of the Nyae-Nyae pans basin. Soils are deep (>1.5 m), pale, acid sands (*c.* pH 4.8) (Table 4.1, page 90).

J. *Cenchrus ciliaris* - *Combretum imberbe* tall, sparse woodland association (Table 3.4, page 49).

This association is characterised by sparsely distributed (1-5 % cover) *Combretum imberbe* trees over ten metres in height (Plate 3.10). Other tree species are absent. Most of the woody plants are multistemmed shrubs. These include *Diospyros lycioides, Maytenus senegalensis, Rhus marlothii* and *Ehretia rigida.* The herbaceous layer is dominated by the perennial grass *Cenchrus ciliaris* which can provide up to 30 % cover at some sites. Where soils are deeper than *c.* 0.2 m, *Enneapogon scoparius* can provide up to 12 % cover. Forbs are predominantly annuals including *Hibiscus calyphyllus, Cleome angustifolia, Sesamum triphyllum* and *Tribulus terrestris.*

This association is restricted in its distribution to the extensive calcrete ridges and hummocks to the west and north of Tsumkwe. Soils are calcareous sands of variable depth (0.2-0.8 m) overlying calcrete boulders and cobbles (Netterburg, 1980) (Table 4.1, page 90).

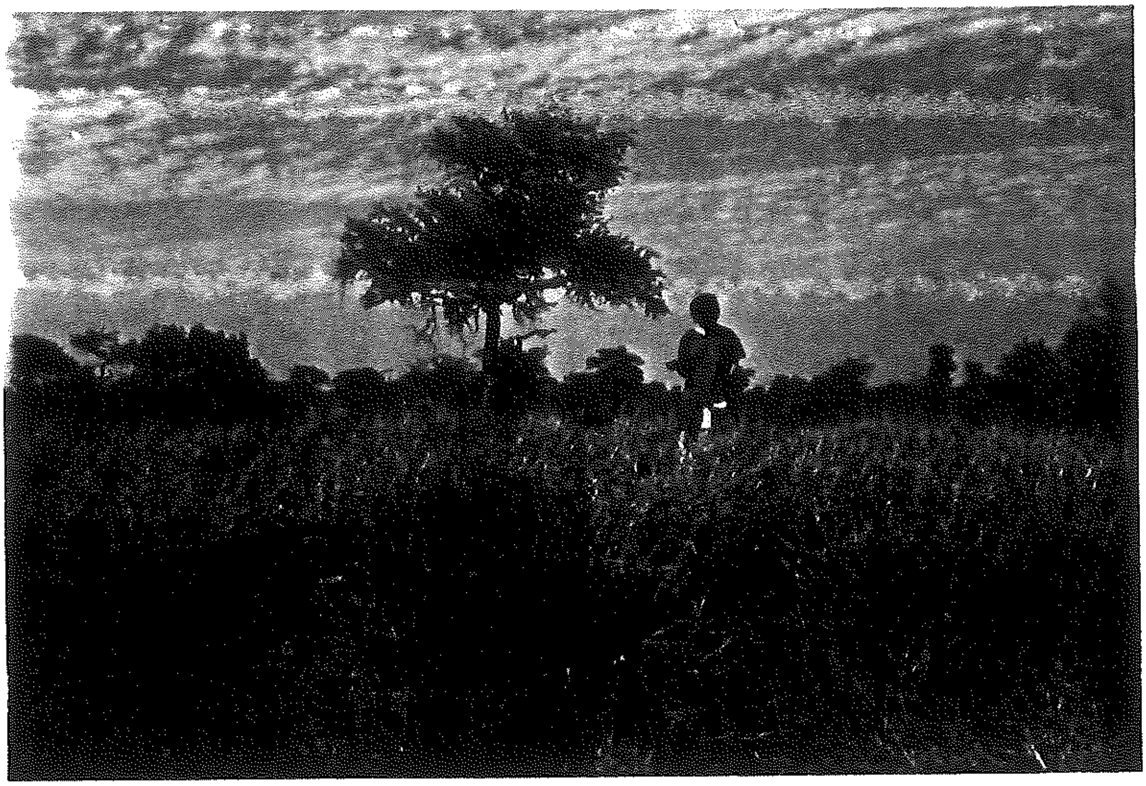


Plate 3.10. *Cenchrus ciliaris - C. imberbe* association. *Cenchrus ciliaris* dominates the herbaceous layer on a low calcrete hummock. *C. imberbe* in the background. No shrubs present at this site.

K. *Grewia flava - Croton grattisimus* closed shrubland association (Table 3.4).

This association is characterised by sparsely (*c.* 1 % cover) distributed trees of *Maytenus senegalensis, Acacia mellifera, Acacia hebeclada* and *Ziziphus mucronata* which are usually less than five metres in height (Plate 3.11). The major woody component consists of the multistemmed shrubs *Grewia flava, Croton grattisimus, Combretum hereroense, Commiphora pyracanthoides, Commiphora africana* and *Rhus tenuinervis*. These shrubs provide dense cover of between 30 % and 60 % and rarely exceed 3 m in height.

Plate 3.11. *Grewia flava - Croton grattisimus* association. A typical stand of *G. flava* (background), *C. grattisimus* (left foreground) and *Catophractes alexandri* (centre).

Grasses provide low cover (1-5 %) in the field layer. *Stipagrostis uniplumis, Enneapogon scoparius, Eragrostis lehmanniana* and *Cenchrus ciliaris* are characteristic. Forbs contribute little to overall cover (<1 %) and there are no characteristic species.

This association is widely distributed in the central basin where calcrete hummocks, ridges and broken hardpan calcretes have a thin covering of soil. Soils are shallow calcareous sands 0.1-0.5 m deep (Table 4.1, page 90).

Two distinct sub-associations of the *Grewia flava* - *Croton grattisimus* association occur. These are:

(i). The *Catophractes alexandri* sub-association. This sub-association is distinct in that *Catophractes alexandri* dominates the woody component with cover values between 20 % and 40 % (Plate 3.12). It is found where shallow soils (<0.15 m) overlie bands of unfractured hardpan calcrete.

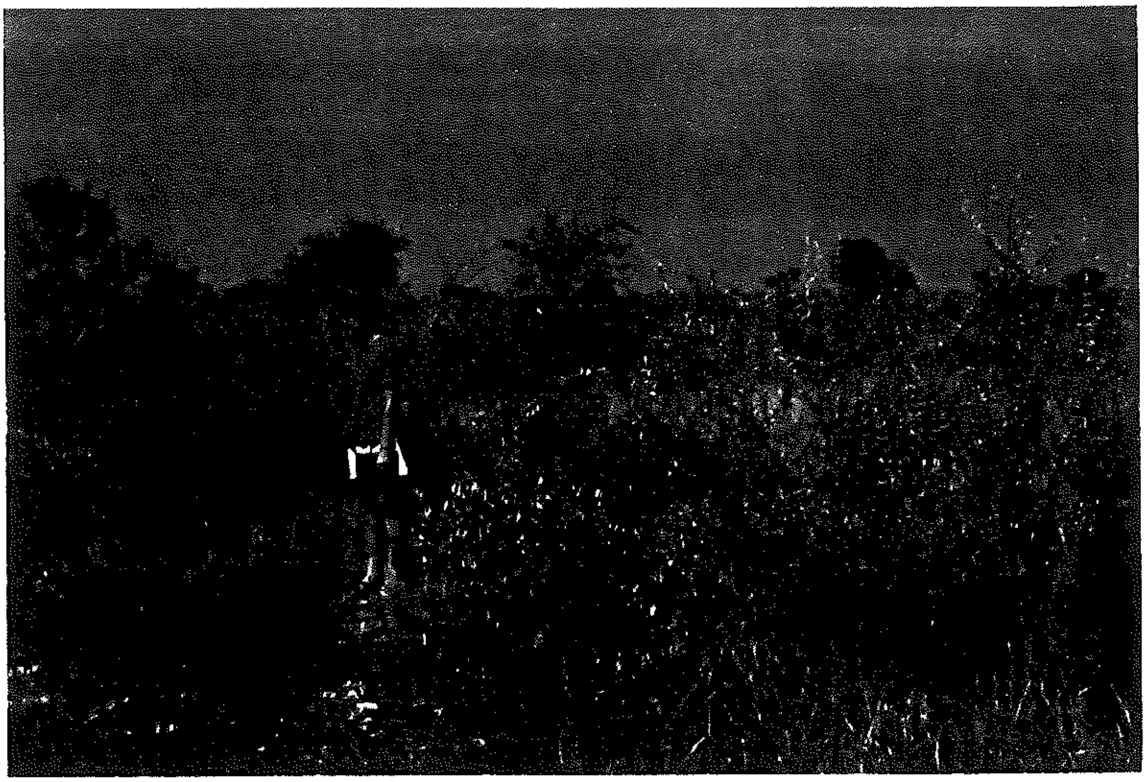


Plate 3.12. *Catophractes alexandri* sub-association. A dense stand of *C. alexandri* on hard pan calcrete.

(ii). The *Acacia mellifera* sub-association. In this sub-association small tree and shrub forms of *Acacia mellifera* dominate the woody component at high cover values (30-60 %) (Plate 3.13). This sub-association occurs throughout the study area, mainly on the margin of pans, along drainage lines and where shallow depressions are subject to periodic flooding during the wet season.

Plate 3.13. *Acacia mellifera* sub-association. A dense stand of *A. mellifera* along the margin of a drainage line. *Chloris virgata* is the dominant grass species.

L. *Combretum apiculatum* tall, closed woodland association (Table 3.4, page 49).

Combretum apiculatum trees, six to ten metres in height with cover values of 15 % to 60 %, dominate the woody component of this association (Plate 3.14). *Acacia fleckii* is the only other dominant tree species, providing between 1 % and 10 % cover.

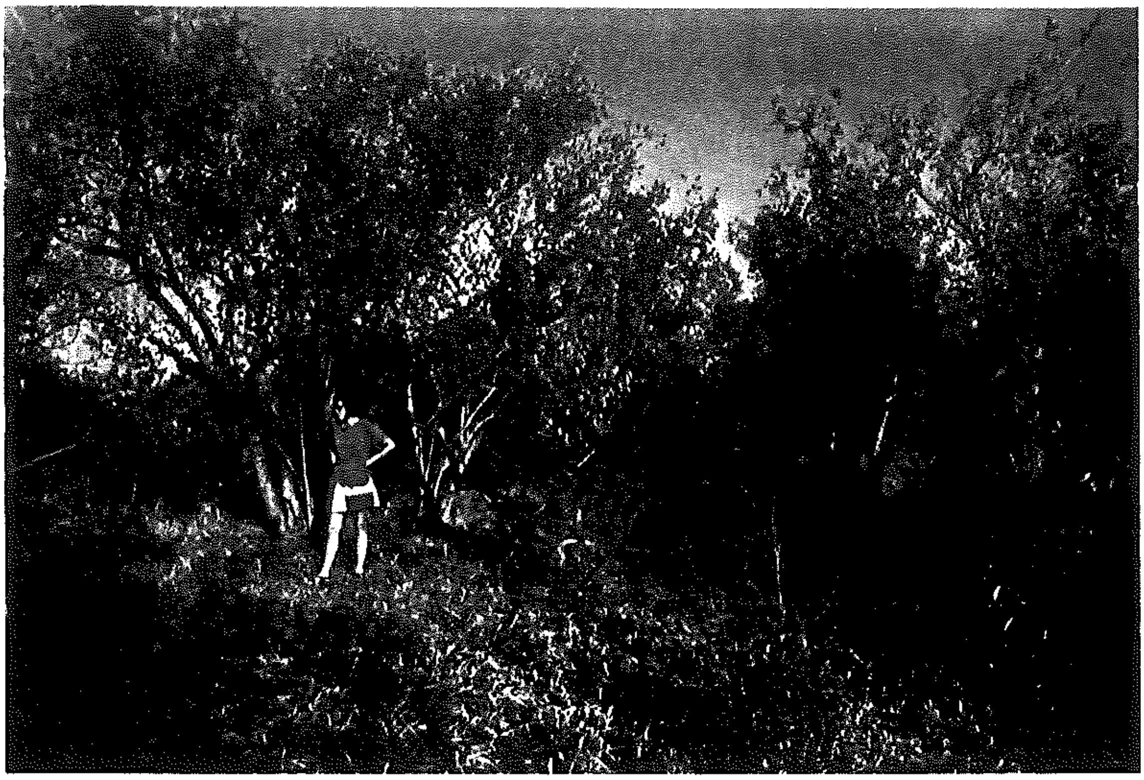


Plate 3.14. *Combretum apiculatum* association. A typical stand of *C. apiculatum* on sandy soils overlying calcrete.

Characteristic of the association is the occurrence of isolated individual trees and small groves of *Adansonia digitata, Sclerocarya birrea* and *Ricinodendron rautanenii* (Plate 3.15).

Plate 3.15. A small grove of *Adansonia digitata and Sclerocarya birrea* in *Combretum apiculatum* woodland. *Ricinodendron rautanenii* (centre background) can also be seen.

A number of shrubs are common in this association, including *Grewia bicolor, Grewia flava, Dichrostachys cinerea* and *Croton grattisimus*. The herbaceous layer is dominated by annual grasses which can provide between 15 % and 40 % cover. Characteristic species are *Aristida rhiniochloa, Aristida effusa, Aristida adscensionis, Urochloa brachyura* and *Eragrostis dinterii*. Perennials such as *Eragrostis nindensis* and *Schmidtia pappophoroides* occur at low cover values (<1 %). Forbs are not well represented. *Commelina forskalaei, Tylosema esculentum, Gisekia africana, Raphionacme lanceolata* and *Sesamum* *triphyllum* all occur widely but at cover values of less than 1 %.

This association is widely distributed in the eastern, central and northern parts of the study area, and is the most extensive vegetation association within the central basin. Soils are medium- to coarse-grained sands of variable depth (0.2->1.5 m) (Table 4.1, page 90).

Plate 3.16. *Commiphora pyrocanthoides* sub-association. Large *C. pyrocanthoides* trees (left, centre) are characteristic of this sub-association.

Subsurface geology is thought to affect the species composition of this association to some degree, as a distinct sub-association occurs where the *Combretum apiculatum* association is underlain by granite east of Tsumkwe. This is the *Commiphora pyrocanthoides* sub-association. The species composition of this sub-association is the same as is described for the association with the exception that *Commiphora pyrocanthoides* occurs commonly as a tree of up to six metres (Plate 3.16) and contributes between 10 % and 30 % cover. It is a co-dominant species with *Acacia fleckii*.

M. *Schmidtia pappophoroides* tall, closed grassland association (Table 3.5, page 63).

Woody species in this association are largely restricted to termitaria. Shrub forms of *Combretum hereroense, Ozoroa paniculosa* and *Grewia flava* are the commonest woody species on the termitaria (Plate 3.17). Within the grasslands, the suffrutex *Elephantorhiza elephantina* is characteristic and occurs at cover values of up to 5 %. Perennial grasses dominate the association and total cover varies from 25 % to 60 %. Highest cover values are contributed by *Schmidtia pappophoroides* (5-30 %), *Brachiaria nigripedata* (1-15 %) and *Digitaria eriantha* (5-25 %). Other perennial species such as *Stipagrostis uniplumis, Anthephora pubescens* and *Heteropogon contortus* occur widely at low cover values (1-5 %). Annual grasses such as *Melinis repens* and *Aristida meriodionalis* all occur at low cover values (1-5 %). Forbs are mainly creepers such as *Ipomoea obscura, Merremia palmata, Citrillus lanatus* and *Vigna decipiens*, and geophytes such as *Ledebouria* spp., *Ornithogalum* spp. and *Ammocharis coranica*.

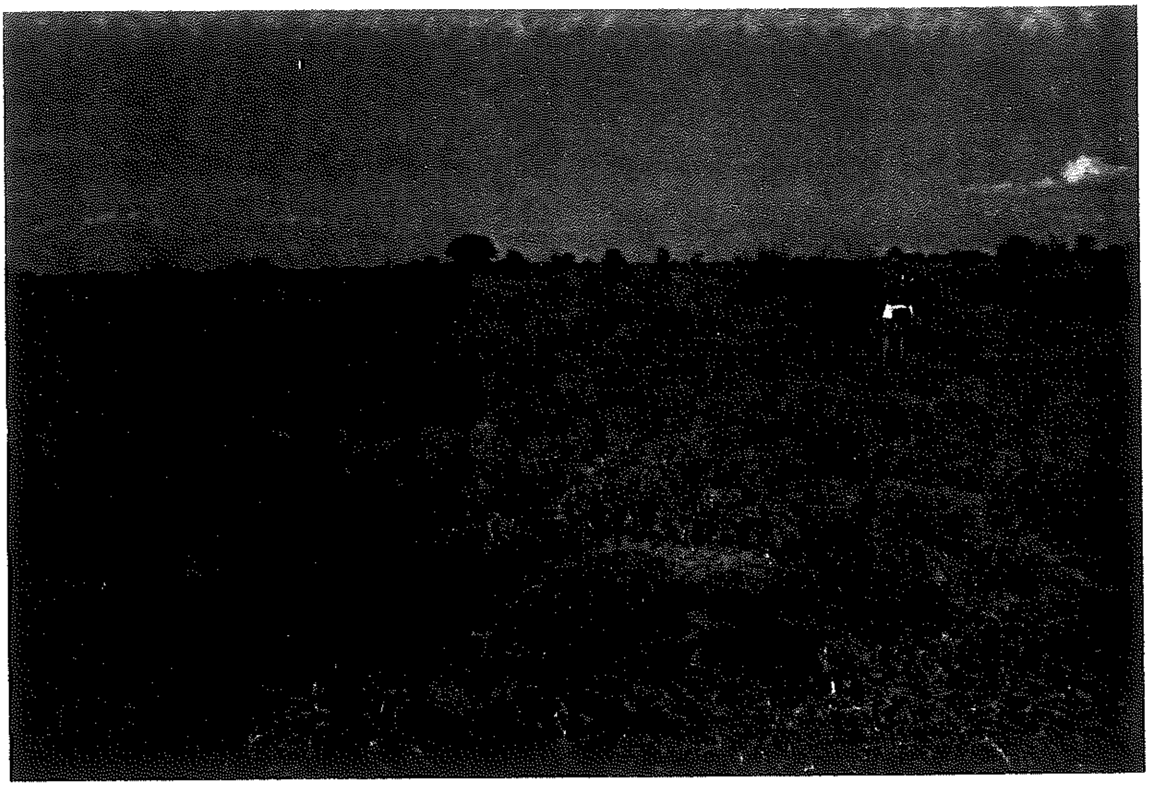


Plate 3.17. *Schmidtia pappophoroides* association. *Schmidtia pappophoroides* dominates these grasslands near Klein Dobe. Note that woody species (largely *Grewia* spp. and *Combretum hereroense*) forms small clumps usually associated with termitaria.

This association occurs widely within the study area. It is found in areas of low relief such as undulating plains and interdune slacks. Soils are coarse grained sands and loamy sands of variable depth (0.4->1.5 m) (Table 4.1, page 90).

Table 3.5 Synoptic frequencies of the characteristic species occurring in Associations M–R. Association groupings generated by TWINSPAN. Key to associations: M = *Schmidtia pappophoroides* grassland; N = *Anthephora pubescens* grassland; O = *Terminalia sericea* – *Bauhinia petersiana* shrubland; P = *Terminalia sericea* – *Combretum collinum* woodland; Q = *Burkea africana* woodland; R = *Baikiaea plurijuga* woodland.

SPECIES	ASSOCIATION					
	M	N	O	P	Q	R
No. of releves	19	17	15	15	10	5
Total No. of species	93	64	98	81	66	52
Combretum hereroense	V	V				
Anthephora pubescens	III	III				
Eragrostis nindensis	III	III				
Grewia flava	III	III			III	
Brachiaria nigripedata	V	V		III		
Ozoroa paniculosa	IV	IV		II		
Elephantorhiza elephantina	IV	IV	III			
Acacia fleckii		III			III	
Lapeirousia vaupeliana		V				
Kyllinga alba		III				
Fimbristylis hispidula		V	III			
Cyperus margaritaceus		IV				
Hermannia tomentosa		IV				
Aristida meriodionalis	IV	IV		III	III	
Schmidtia pappophoroides	V	V	III	IV	V	V
Digitaria eriantha	V	V	IV	IV	IV	
Melinis repens	III	IV	III	III		III
Stipagrostis uniplumis	IV	V	III	IV	V	V
Oxygonum alatum		III	IV			
Limeum fenestratum		IV	V			
Grewia bicolor			IV		IV	
Eragrostis pallens			IV	IV	V	
Panicum kalaharense			IV	IV	IV	
Burkea africana			III	V	IV	
Lonchocarpus nelsii			IV	IV	III	
Ochna pulchra			II	IV	IV	
Pogonarthria squarrosa				III		
Combretum zeyheri				II	III	
Eragrostis dinteri		III		IV	III	V
Bauhinia petersiana			IV	IV	IV	V
Terminalia sericea			V	V	V	IV
Dichapetalum cymosum			III		IV	III
Grewia retinervis			III		II	IV
Baphia massaiensis				II	V	V
Baissea wulfhorstii				V	IV	IV
Evolvulus alsinoides				IV	III	IV
Combretum collinum				V	V	IV
Aristida stipitata				III	IV	V
Pterocarpus angolensis					III	
Eragrostis rigidior	III				IV	
Dichrostachys cinerea					IV	
Tricholaena monachne					III	III
Croton gratissimus					IV	V
Combretum psidioides					IV	IV
Combretum englerii					III	IV
Commiphora angolensis						IV
Acacia ataxacantha						V
Baikiaea plurijuga						V

N. *Anthephora pubescens* tall, closed grassland association (Table 3.5, page 63).

This association has a sparse cover (1-5 %) of the shrubs *Combretum hereroense, Dichrostachys cinerea, Ozoroa paniculosa* and *Terminalia sericea*, which also occurs as a small tree (<3 m) (Plate 3.18). Woody species are not restricted in their distribution to termitaria.

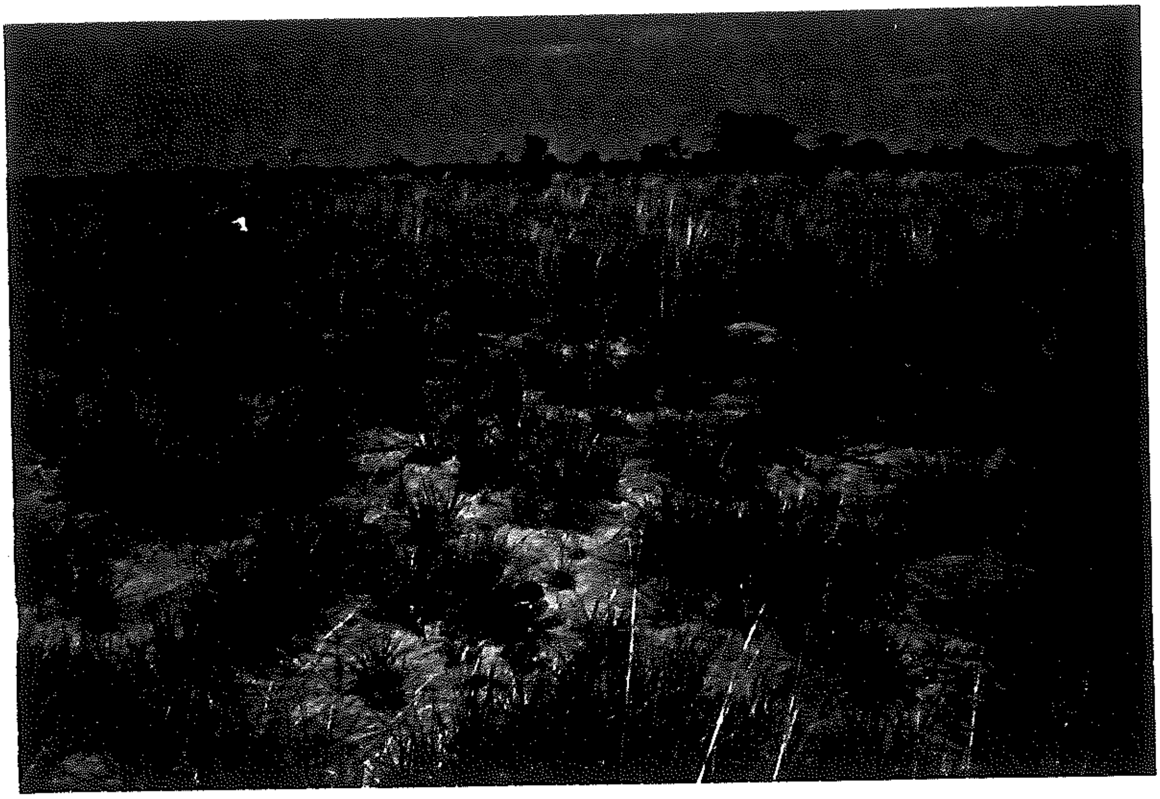


Plate 3.18. *Anthephora pubescens* association. Typical grassland on deep Kalahari sand dominated by perennial species such as *Digitaria eriantha, Anthephora pubescens* and *Brachiaria nigripedata*. *Schmidtia pappophoroides* is common but seldom dominant. Note the heavily leached soils.

Perennial grasses dominate the herbaceous layer and most species are common to both this association and the

Schmidtia pappophoroides association. This association is characterised by the presence of *Eragrostis nindensis* and *Eragrostis rigidior* at low cover values (1-5 %), and *Anthephora pubescens* occurring at higher cover values (5-12 %) than in the *Schmidtia pappophoroides* association (M). Annual grasses other than *Aristida meriodionalis* have low frequencies and low cover values (<1 %). Forbs are well represented, with the perennials *Vigna decipiens, Neorautanenia mitis, Aptosimum decumbens* and several root parasites such as *Alectra parvifolia* and *Striga gesnerioides* being common.

This association occupies deep (>1.5 m), sandy soils throughout the study area. It is primarily associated with Kalahari sand deposits and is common in the north of the study area and to the south of the Aha Hills. Soils are leached, coarse-grained sands (Table 4.1, page 90).

O. *Terminalia sericea - Bauhinia petersiana* high, closed shrubland (Table 3.5, page 63).

Shrubs and small trees are characteristic of this association and can give total cover values of 25-60 %. *Terminalia sericea* contributes between 15 % and 40 % cover and seldom exceeds three metres in height, as does *Lonchocarpus nelsii* (Plate 3.19). A distinct shrub stratum one to two metres in height composed of *Bauhinia petersiana, Ochna pulchra* and *Dichrostachys cinerea* is normally present. The poisonous shrub *Dichapetalum cymosum* is commonly found in this association.

Plate 3.19. *Terminalia sericea - Bauhinia petersiana* association. A dense stand of *T. sericea* and *B. petersiana* (left foreground). Grasses present include *Eragrostis pallens* and *Panicum kalahariense*.

Panicum kalahariense, Eragrostis pallens, Stipagrostis uniplumis and *Schmidtia pappophoroides* are characteristic perennial grasses. Forbs are mainly annuals and geophytes such as *Limeum fenestratum, Oxygonum alatum, Acanthosicyos naudiniana, Lapeirousia vaupeliana* and *Lophiocarpus tennuissimus*.

This association is widely distributed within the study area, but is restricted to areas of Kalahari sand deposits. Soils are well drained, deep (>1.5 m), coarse-grained sands which show evidence of leaching, the upper 0.2 m being considerably paler than the rest of the profile (Table 4.1, page 90).

P. *Terminalia sericea - Combretum collinum* short, closed woodland association (Table 3.5, page 63).

This association is dominated by *Terminalia sericea* trees three to five metres in height at high cover values (15-40 %) (Plate 3.20). The presence of *Combretum collinum* at cover values of 5-25 %, *Combretum zeyherii* and *Combretum psidioides* at low cover values (1-5 %) clearly differentiates this association from the *Terminalia sericea - Bauhinia petersiana* association (O) described above. *Burkea africana* is common as a small shrub below one metre. Grasses dominate the herbaceous layer, with the perennials *Schmidtia pappophoroides, Digitaria eriantha* and the annual *Eragrostis dinterii* having the highest frequencies of occurrence. There are no characteristic forbs in this association.

This association is widely distributed in the north of the study area, where it is found on the lower slopes of linear dunes and more extensively on flat areas composed of Kalahari sand deposits. Soils are deep (>1.5 m), coarse-grained sands which show evidence of leaching in the upper 0.2 m (Table 4.1, page 90).

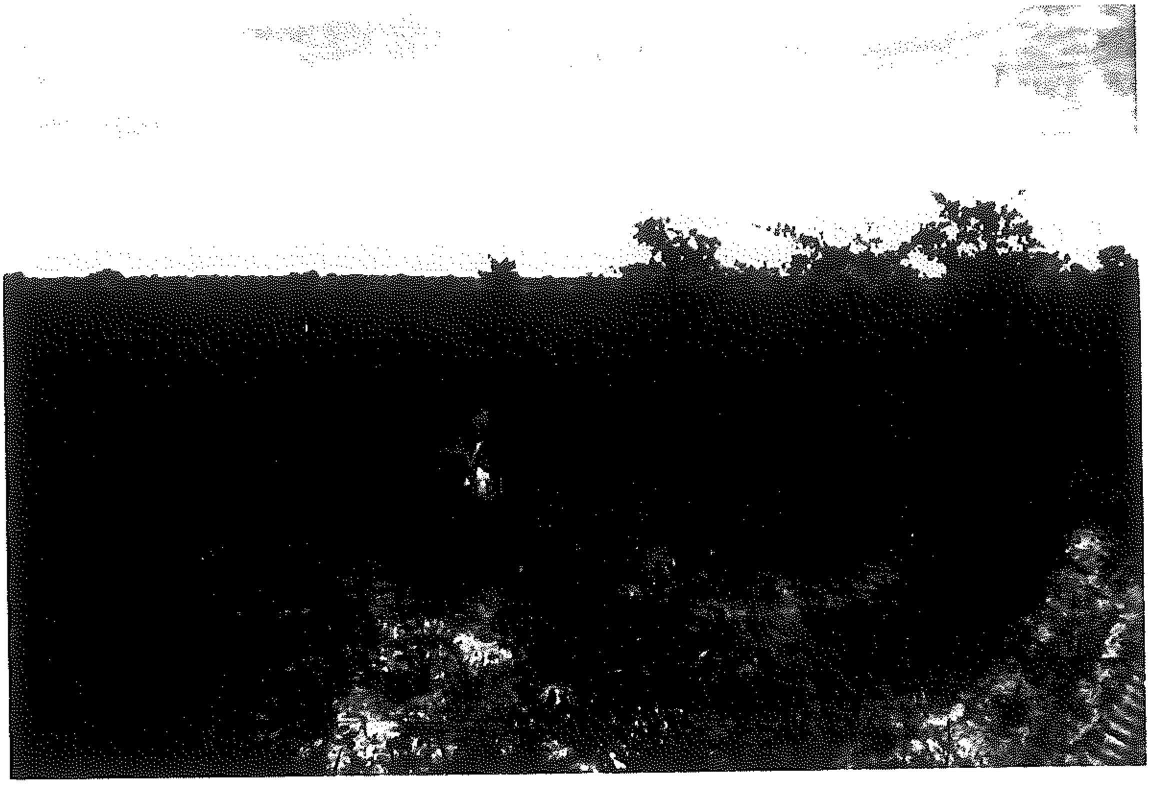


Plate 3.20. *Terminalia sericea - Combretum collinum* association. A dense stand of *T. sericea, C. collinum* and *Bauhinia petersiana*. Note the heavily leached sandy soils.

Q. *Burkea africana* tall, closed woodland (Table 3.5, page 63).

The woody component of this association is clearly stratified. *Burkea africana* trees over ten metres in height dominate the taller stratum (Plate 3.21). Also characteristic, are large, isolated *Pterocarpus angolensis* trees (>10 m). *Terminalia sericea, Lonchocarpus nelsii* and *Combretum collinum* form a distinct understorey of small trees below five metres. The shrub layer is characterised by *Diplorhynchus condylocarpon, Ochna* *pulchra, Bauhinia petersiana* and *Baphia massaiensis* at low cover values (1-5 %).

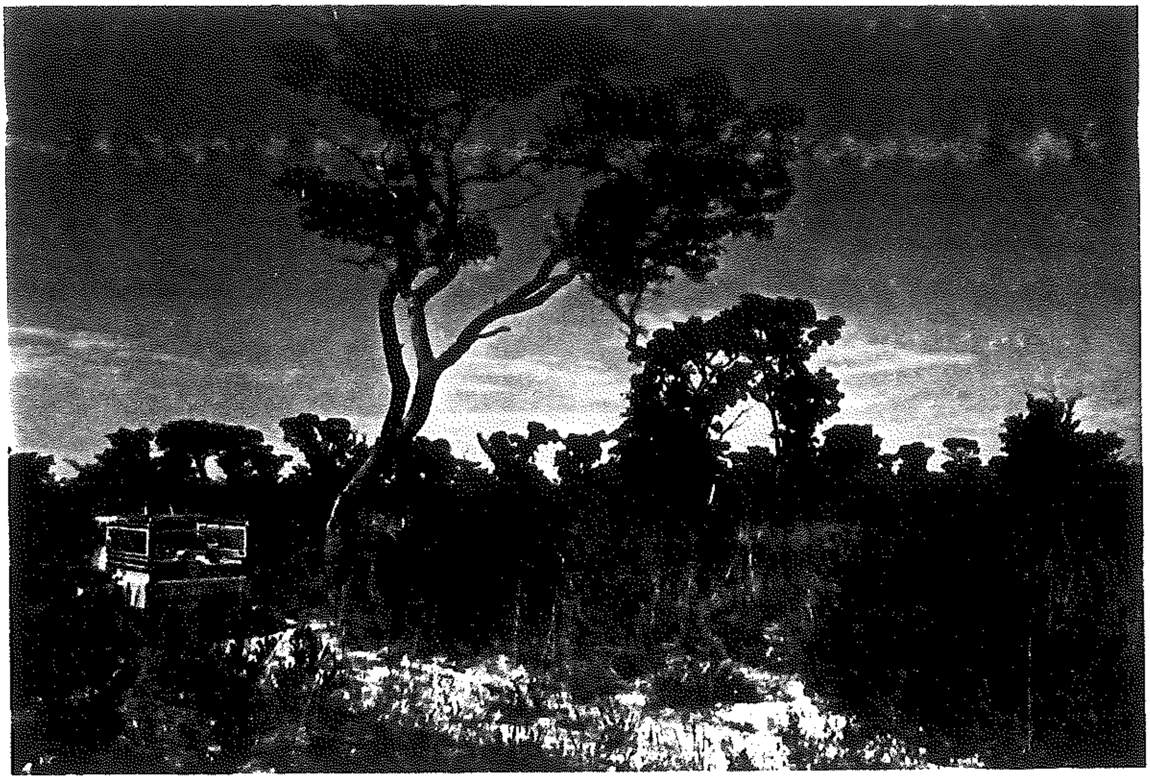


Plate 3.21. *Burkea africana* association. This association is usually well stratified with *B. africana* dominant over 10 m. The understorey is characterised by *Terminalia sericea, Baphia massaiensis* and *Bauhinia petersiana*.

Perennial grasses dominate the herbaceous layer and *Schmidtia pappophoroides, Aristida stipitata* and *Panicum kalahariense* are all characteristic. Forbs are common and are generally widespread species. These include *Baissea wulfhorstii, Acrotome inflata, Hemizygia bracteosa* and *Evolvulus alsinoides*.

This association is found only on Kalahari sand deposits and is widely distributed throughout the study area. It is most extensive in areas of flat topography but also occupies sites on the slopes of linear dunes. Soils are deep (>1.5 m) well drained, dystrophic sands (Table 4.1, page 90).

R. *Baikiaea plurijuga* high, closed woodland association (Table 3.5, page 63).

The woody component of the association is dominated by large (10-20 m), tall trees of *Baikiaea plurijuga* which form dense stands with cover values between 30 % and 75 % (Plate 3.22). *Commiphora angolensis, Baphia massaiensis, Combretum engleri* and *Acacia ataxacantha* form a distinct layer of small trees and shrubs below 4 m. The herbaceous layer is sparse (<10 % total cover) and there are few species present.

This association is limited both in extent and distribution within the study area. It occupies the crests of large (15-25 m in height), linear dunes in the north of the study area and occurs in discrete patches associated with deep sand deposits in the west of the study area. Soils are deep (>1.5 m), coarse-grained sands which show evidence of leaching (Table 4.1, page 90).

Plate 3.22. *Baikiaea plurijuga* association. A typical stand of *B. plurijuga* and *Commiphora angolensis* (centre, right) on a dune crest. The herbaceous layer is unusually dense, with most of the cover provided by *Tricholaena monachne* and *Eragrostis dinteri*. Shrubs include *Baphia massaiensis, Acacia ataxacantha* and *Combretum engleri*.

3.4 DISCUSSION

3.4.1. *The Braun-Blanquet technique.*

Although the Braun-Blanquet approach to the classification of vegetation has been widely criticised regarding the subjectivity of site selection, the imprecision of measurement of habitat factors and the requirement of considerable knowledge of the vegetation being sampled (see Mueller-Dombois & Ellenberg (1974) and Moore & Chapman (1986) for a review), it proved to be very useful and applicable in this study.

In this study a clear idea of the plant associations and their floristic and habitat relationships was obtained, indicating the discontinuities in the floristic response of vegetation to the environment. Despite the problems of definition where habitat/vegetation units intergrade (e.g. those associations in the "Kalahari Sand" areas), the tables (Tables 3.3, 3.4, 3.5) revealed the existence of reasonably discrete associations and the floristic relationships between them. This satisfies the requirement of Coetzee & Werger (1975) that the classification system should clearly reflect the response of vegetation to environmental factors at all hierarchical levels and that the units distinguished be readily recognisable in the field. That is, they should not be synthetic abstractions, but should show a degree of "reality".

These "real" vegetation units can be compared to vegetation classified in other areas. This provides valuable insights into the possible environmental determinants of individual units.

3.4.2. *The associations.*

Those associations which occur on the deep aeolian Kalahari sands show distinct similarities with syntaxa described in other studies of the Kalahari vegetation.

The dominant and characteristic species in the *Baikiaea plurijuga* association (R) are largely the same as those described for *Baikiaea* woodlands in Zambia (White, 1965; Cole, 1986), Zimbabwe (Rushworth, 1975; Childes & Walker, 1987) and northern Namibia (Giess, 1971).

The *Burkea africana* association (Q) is characterised by a number of species which are common to similar syntaxa described in Zimbabwe (Childes & Walker, 1987), on the Omuverume and Waterberg Plateaux of central Namibia (Rutherford, 1972) and Nylsvlei in the northern Transvaal, South Africa (Coetzee *et al.*, 1976).

The *Terminalia sericea - Combretum collinum* (P) association contains the same dominant and co-dominant species as the *Terminalia sericea* scrub described by Childes and Walker (1987) in Hwange National Park. Studies in the southern Kalahari System have described syntaxa which compare closely to the *Terminalia sericea - Bauhinia petersiana* association (O) (Leistner & Werger, 1973; Cole & Brown, 1976; Skarpe, 1986), as have studies in other parts of southern Africa; for example, Rutherford

(1972) - Omuverume & Waterberg Plateaux; Coetzee *et al.* (1976) - Nylsvlei; le Roux *et al.* (1988) - Etosha National Park, Namibia.

Comparison of the central basin associations is difficult, as many of these associations are of limited extent within the study area. There are, however, a number of syntaxa described from other areas that have species compositions similar to the associations described in this study.

The *Acacia kirkii* association (A) is known from bottomland sites in Etosha National Park (le Roux *et al.*, 1988), as is the *Sporobolus coromendalianus* (E) association, which is also described from areas in the southern Kalahari (Leistner & Werger, 1973). Skarpe (1986) and le Roux *et al.* (1988) describe vegetation types that have similar species compositions to the *Odyssea paucinervis* association (B) from the southern Kalahari and Etosha National Park, respectively.

The *Acacia luederitzii* (C), *Combretum apiculatum* (L), *Acacia erubescens* (H) and *Terminalia prunioides* (G) associations compare closely with syntaxa described from the Kalahari System south of the Bakalahari-Schwelle by Cole & Brown (1976), Cole & le Roux (1978) and Cole (1986). The *Catophractes alexandri* sub-association of the *Grewia flava - Croton grattisimus* association (K) is described by Skarpe (1986) and Cole & Brown (1976) from the same area where it is more extensive than in eastern Bushmanland.

The *Terminalia prunioides* association (G) is also described from the Kalahari System in Zimbabwe (Childes & Walker, 1987).

The constituent species of the grassland associations (M, N) are listed in many of the vegetation studies cited above, but only Skarpe (1986) and Cole & Brown (1976) describe vegetation units which compare with the species composition of the *Schmidtia pappophoroides* association (M).

3.4.3. *The conservation value and status of the study area.*

Menaut (1983) calculated that the Kalahari Domain (undefined in Menaut) of the Sudano-Zambezian Region (Figure 3.2, page 80) has the lowest number of species per 10 000 km^2 (1020) of all phytochorological units in Africa. Other authors (Lebrun, 1960: in Skarpe, 1986; White (1971)) also refer to the "impoverished" Kalahari flora. These comments are made without reference to the importance of environmental conditions in determining the composition and distribution of the vegetation units and the general paucity of botanical work done within the

Kalahari System.

Two factors - harsh environmental conditions and low niche separation - are important in determining the low species diversity of the Kalahari Domain. Harsh environmental conditions (in this case erratic, low rainfall, high temperatures, high evaporative demand and poor soil nutrient conditions) are thought to give rise to species poor communities (Whittaker, 1972). The uniformity of habitat in areas covered by Kalahari sand (areas of deep dystrophic sands with little relief) provides low niche separation (Diamond, 1984; Skarpe, 1986) and hence, low species numbers. Species adapted to the environmental conditions are found to have wide geographic distributions within the Kalahari System (e.g. *Terminalia sericea*).

In this study no plant species or vegetation associations were found to have their distributions limited to, or centred on, eastern Bushmanland. The total number of species recorded in each association was low (White, 1983), with totals ranging from 20 in the *Odyssea paucinervis* association (B) to 114 in the *Combretum apiculatum* association (L) (Tables 3.3, 3.4, 3.5).

For the majority of associations there are similar phytosociological syntaxa described from areas. These are widely separated geographically within the savanna biome of southern Africa (*sensu* Huntley, 1982) and, in many cases, fall within established conservation areas. These include Etosha National Park (le Roux *et al.*, 1988), Hwange National Park (Childes & Walker, 1987), Kalahari Gemsbok National Park (Leistner & Werger, 1973) and Nylsvlei Nature Reserve (Coetzee *et al.*, 1976).

At present eastern Bushmanland has no conservation status within Namibia. As the majority of species and associations occur elsewhere within southern Africa, the area has a low conservation priority according to evaluation guidelines established by the IUCN (1980). The question of conservation priority changes, however, if the study area is considered, not in isolation, but in relation to the regional context of the Kalahari System as a whole. As far as can be ascertained from the literature, the number of species and associations is higher than any other area of similar size within the Kalahari System (Table 3.6). In this respect eastern Bushmanland rates a high conservation priority (IUCN, 1980). In addition, the vegetation can be considered unique (*sensu* IUCN, 1980) in that several associations and species reach their distributional limits in the area (e.g. *Baikiaea plurijuga* association (R)), while others (e.g. *Acacia kirkii* association (A)) are rare within the Kalahari.

Table 3.6 Comparative table of the number of species and associations found in selected study areas within the Kalahari System.

Study Area	Size (km^2)	No. of Associations	No. of species	Reference
Bushmanland	7000	18	438	1
Hwange National Park	?	9	228*	2
Kalahari National Park	9590	10	444	3
Ghanzi Ridge	c.18000	9	458	4
Southern Kalahari	>100000	16	?	5

References: 1 - This study; 2 - Childes & Walker (1987):*Species count from Rushworth (1975); 3 - Leistner & Werger (1973); 4 - Cole & Brown (1976); 5 - Skarpe (1986). No size given for Hwange study area by Childes & Walker (1987)

3.4.4. *Phytogeography and chorology.*

During the early years of phytogeographical study in Africa, the boundaries of chorological units were distinguished on the basis of fragmentary collections and as a result were often expressions of opinion rather than fact. Historically, botanical information regarding the Kalahari has been sparse and it is only recently that the phytogeographical boundaries and chorological affinities of the Kalahari are being clarified.

The major phytochorological units of southern Africa are illustrated in Figure 3.2. The vegetation of the Kalahari System south of the Bakalahari-Schwelle has been shown to have strong phytochorological affinities with the Karoo-Namib Region (*sensu* White, 1965) (Leistner, 1967; Werger, 1973; Skarpe, 1986). Several studies have shown the northern Kalahari (i.e. north of the Bakalahari-Schwelle) to have closer floristic affinities with the Zambezian Domain of the Sudano-Zambezian Region (*sensu* White, 1965) than with the Karoo-Namib Region (Volk, 1965; White, 1971; Werger & Coetzee, 1978) (Figure 3.2). The study by Menaut (1983) accords with this division of the Kalahari System. However, a study by White (1983) excludes much of the northern Kalahari (in which the study area is located) from the Zambezian Domain of the Sudano-Zambezian Region (Figure 3.2).

Divisions of classification are by necessity somewhat subjective, but, based on the floristic data of the present study, the divisions proposed by White (1983) are debatable in that the flora of the study area is dominated, not by the genus *Acacia* as proposed by White, but by broad-leafed species of distinct Zambezian origin. Species such as *Burkea africana, Commiphora angolensis, Pterocarpus angolensis, Bauhinia petersiana* and *Ricinodendron rautanenii*, listed as characteristic in the Zambezian Domain (White, 1983), all occur commonly within the study area and up to 200 km south of the study area

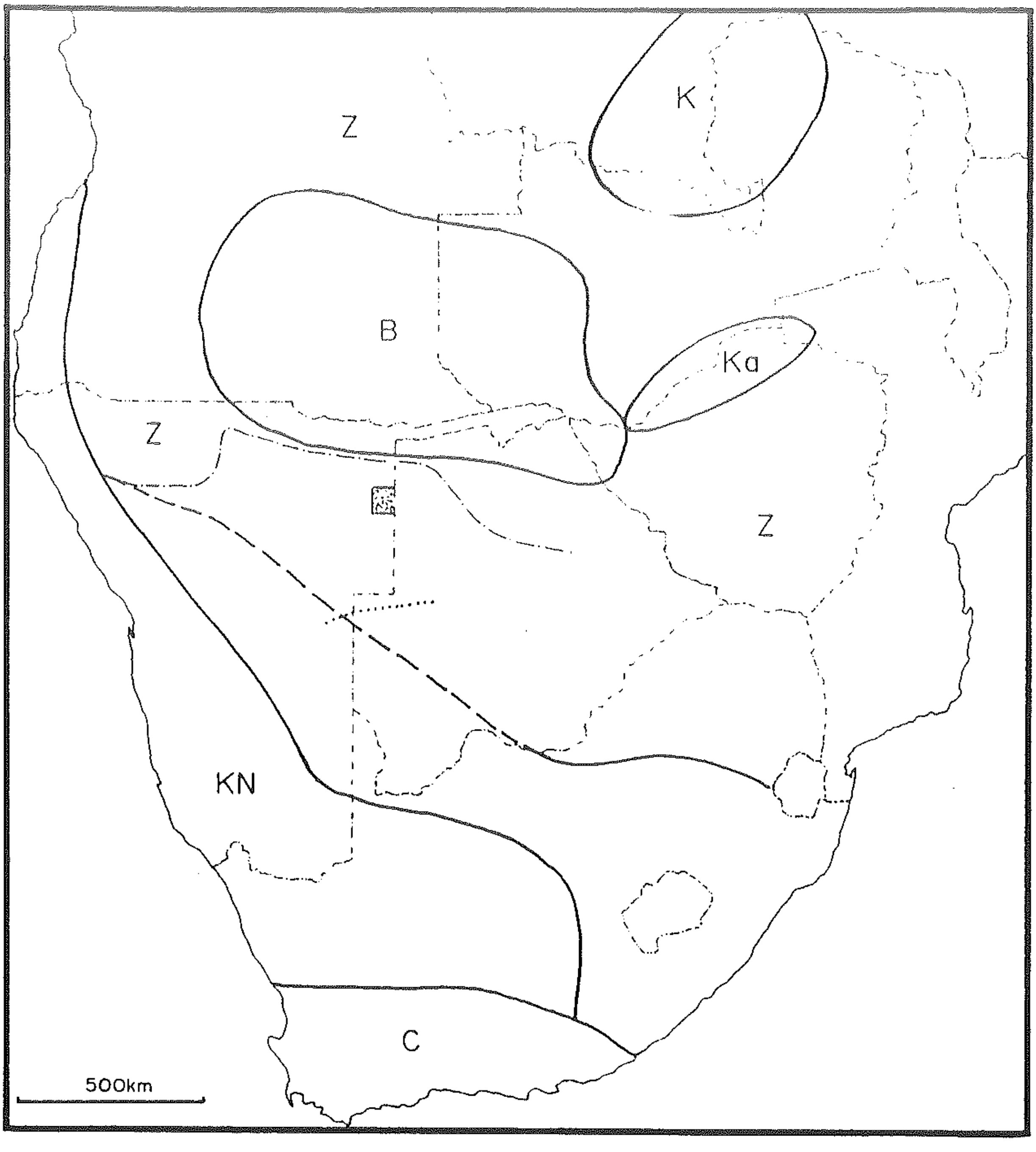


Figure 3.2 Map of southern Africa showing the position of the study area (stippled) in relation to Whites' (1965) major phytochrological regions. Z = Zambezian Domain of the Sudano-Zambezian Region, containing three centres of endemism, K = Katangan, B = Barotse and Ka = Kariban. KN = Karoo-Namib Region, C = Cape Region. Whites' (1965) transitional boundary between the Karoo-Namib Region and the Zambezian Domain is shown (— —) as is Whites' (1983) limit of the Zambezian Domain (-·-·—). The position of the Bakalahari-Schwelle is indicated by the dotted line.

(Volk, 1965; Correira & Bredenkamp, 1987; personal observation). The boundary originally proposed by White (1965) (Figure 3.2) reflects the phytochorological affinities of vegetation of the study area more accurately than his later work (White, 1983).

The confusion regarding the phytochorological affinities of the study area emphasises the poor state of knowledge of the flora of the Kalahari System. As Huntley (1982) suggests, further analysis of the Kalahari flora in the Sudano-Zambezian Region may lead to the identification of a new "Austral" Domain centred on Botswana.

3.5 CONCLUSION

The Kalahari Domain (*sensu* Menaut, 1983) is regarded by a number of authors as having an "impoverished" flora (White, 1983; Skarpe, 1986). The harsh environmental conditions and the extensive cover of a largely uniform sand overburden providing low niche separation, are two of the factors thought to contribute to this species-poor flora.

Eastern Bushmanland has a surprising diversity of associations and species for an area of its size within the Kalahari System. The total assemblage of associations and species can be viewed as unique within the Kalahari

System. A number of the associations and species reach their distributional limits in the study area while others are rare within the Kalahari System.

The majority of species and associations, however, are widely distributed in the savanna biome of southern Africa, many occurring beyond the limits of the Kalahari System. Although the assemblage of associations and species is unique within the Kalahari, the determinants of the system are likely to be common to the savannas. The vegetation of eastern Bushmanland is therefore, likely to be an expression of a unique (within the Kalahari System) set of environmental determinants.

The manner in which environmental determinants of savannas such as climate, geomorphology, geology and soil forming processes, interact to determine vegetation distribution, structure and composition in eastern Bushmanland is the subject of Chapter Four.

CHAPTER FOUR

ENVIRONMENTAL DETERMINANTS OF THE DISTRIBUTION, STRUCTURE AND COMPOSITION OF THE VEGETATION ASSOCIATIONS

4.1 INTRODUCTION

Cole (1982 & 1986) hypothesised that the structure of savanna components (trees, shrubs and grasses) is influenced largely by soil moisture conditions, while the composition of vegetation units (e.g. associations) varies with the nutrient status of the soils. Soil moisture and nutrient availability are in part dependent on soil type and structure, which in turn may be related to bedrock geology (Venter, 1986) and to superficial deposits, such as aeolian sand and weathering products such as calcrete (Cole, 1982 & 1986; Donahue *et al.*, 1983).

Vegetation associations consequently can have complex distributions which reflect their relationships to edaphic conditions (Bredenkamp, 1985; Cole, 1986; le Roux *et al.*, 1988; Schlesinger *et al.*, 1990). These distributions are related to past and present climatic changes and conditions (Axelrod & Raven, 1978; Cole, 1986; Partridge, 1990; Partridge *et al.*, 1990), the geomorphological evolution of the landscape (Gertenbach, 1983; Cole, 1986), the exposure of geological strata (Cole, 1986) and the short term effects of grazing, fire and man's cultural practices (Bouliere & Hadley, 1983; Walker, 1985b; Frost & Robertson, 1985).

Within the semi-arid regions of southern Africa, savannas have considerable economic significance because of their value as grazing lands. Management and development strategies in these regions are complicated by periodic droughts and the highly variable spatial and temporal distributions in rainfall, which result in pronounced differences in vegetation growth between and within years (Kelly & Walker, 1976; Westoby *et al.*, 1989).

The sustainable utilisation of the vegetation resources for secondary production of either domestic livestock or wildlife, inevitably involves some degree of manipulation and modification of the ecosystem (Child *et al.*, 1984). If resources are to be conserved and their production potential maintained, it is important to understand the natural limitations on their sustainable use. It is, therefore, essential to clarify the determinants of, and the environmental constraints on, the resources.

The aim of this chapter is to relate the distribution, composition and structure of the vegetation associations described in the Chapter Three to underlying environmental gradients determined from floristic and physico-chemical soils data, in the context of Cole's (1986) hypothesis. A generalised model of the environmental factors determining the vegetation characteristics in eastern Bushmanland is developed using information from the analysis of the floristic and soils data. The model is used as the basis for discussion of the utilisation of the vegetation resources within the study area.

4.2 METHODS

4.2.1 *Survey methods.*

Floristic data were collected from 224 sites in the manner described in Section 3.2.1, page 29.

Soil samples were collected at 219 sites. No samples were collected at the *Acacia kirkii* association sites as these were included in the study at a late stage. Soil pits (1 m x 1 m x 1 m) were dug at seven sites to determine the major soil forms (MacVicar *et al*., 1977) and horizon development. Augured holes with a maximum depth of 1.5 m (the length of the augur) were used to determine soil profiles at all sites. Soil samples for analysis were taken from the 0.2-0.3 m fraction of augured holes.

Two litre samples of soil were placed in plastic bottles in the field and these were then oven dried at 60 °C and sieved through a two millimetre gauge sieve when dry. Samples were analyzed at a commercial laboratory (Scientific Services C.C.) in Windhoek. The soil variables determined were: percentages of sand, silt and clay; pH; calcium; magnesium; potassium; sodium; phosphorus. Standardised techniques followed by the Fertiliser Society of South Africa were adopted and 191 soil samples were analyzed. The Bray-1 technique was used for the determination of phosphorus concentrations (Donahue *et al.*, 1983).

4.2.2 *Data analysis.*

4.2.2.1 Floristic data.

The floristic cover-abundance data were ordinated using detrended correspondence analysis (DCA) (DECORANA: Hill, 1979b). Detrended correspondence analysis is an eigenvector ordination technique which ordinates simultaneously both the species and the sites by a re-iterative weighting procedure (Gauch, 1982). It is computationally similar to principal components analysis (PCA) and ordinations of standardised data often produce results very similar to PCA (Gauch, 1982). Detrended correspondence analysis, however, has been found to be more suitable than PCA in displaying floristic gradients (which are often derived from non-standardised data) (Gauch, 1982; Greig-Smith, 1983; Whittaker, 1987).

Detrended correspondence analysis has another feature which makes interpretation of floristic gradients easier than other ordinational techniques. In DCA, the axes are rescaled statistically, with the practical result that equal distances in the ordination correspond to equal differences in species composition (Gauch, 1982).

Ecologically meaningful gradients have been extracted from floristic data collected under a wide variety of field conditions (Gauch, 1982; Greig-Smith, 1983; McDonald, 1987; Whittaker, 1987). The robustness of the statistical assumptions, freedom from distortion of axes and the meaningful axis units used in DCA make it a powerful tool in the interpretation of environmental gradients in floristic data. Peet *et al*. (1988) state, "Detrended correspondence analysis is one of the most powerful multivariate tools available for representing pattern in communities".

All species occurring fewer than three times in the data set were omitted, as these created "noise" (*sensu* Greig-Smith, 1983) and tended to obscure association groupings in relation to the DCA gradients.

Only DCA scores for Axes 1 and 2 are presented, as eigenvalues for these axes were close to unity (1) in all runs performed on the data. Units shown are species halfchanges (SD units) (Gauch, 1982).

4.2.2.2 Soil data.

Principal Components Analysis (PCA) was used to ordinate the ten soil variables for each sample site. Principal components analysis was used in the analysis of soil data as it has been shown to be more suitable for these type of data than DCA (Gauch, 1982).

The soil data were grouped according to the vegetation association into which a sample site fell and summary statistics for each association are given in Table 4.1.

Individual soil variables were tested for significant differences among means (using a t-test not assuming constant variance in the data), in order to highlight extreme values. It was felt that these significantly different values provide important insight into factors determining the distributions of individual associations and species.

In the text associations are referred to by species name(s) and letter given in Chapter Three (e.g., *Acacia kirkii* (A)). In the figures and table the associations are referred to only by the assigned letter with the full name being given in the legend.

4.3 RESULTS

4.3.1 *The soil physico-chemical variables.*

Table 4.1 presents the mean values, ranges and standard errors of soil physico-chemical variables for each of the vegetation associations and sub-associations. Soil depths recorded in Table 4.1 refer to the depth to basal rock or to a pan horizon in the soil.

Soils are predominantly sands and loamy sands. The soils of the "Kalahari Sand" area are more acid (pH 4.8 - 5.7) than those recorded in the "Central Basin" (pH 6.2 - 8.5). "Kalahari Sand" soils are classified as Clovelly, Fernwood and Hutton Forms (MacVicar *et al.*, 1977) and all have high infiltration potentials (*i.e.* low run-off potentials) (Schulze, 1985). "Central Basin" soils are predominantly Mispah and Estcourt Forms which have high to moderately high run-off potentials (Schulze, 1985).

Soil mineral concentrations are low except for calcium, as a result of the high sand fraction in the soils. Mineral concentrations are generally higher in the soils of the "Central Basin" associations, compared with those associations found in the "Kalahari Sand" areas

Table 4.1. Physico-chemical characteristics of soils from identified vegetation associations in eastern Bushmanland. Key: Unit of measure for Ca, Mg, K, Na and P = μmol.g^{-1}. x = mean, se = standard error. Significant differences among means were determined using a t-test not assuming constant variance in the data, * = p <0.005, ** = p <0.05. ASSOC = Association. Key to the associations: B = *Odyssea paucinervis* grassland; C = *Acacia luederitzii* - *Combretum hereroense* woodland; D = *Combretum imberbe* - *Melinis repens* woodland; E = *Sporobolus coromendalianus* grassland; F = *Sansevieria pearsonii* - *Croton menyhardtii* thicket; G = *Terminalia prunioides* woodland; H = *Acacia erubescens* woodland; I = *Acacia erioloba* - *Eragrostis jeffreysii* woodland; J = *Cenchrus ciliaris* - *Combretum imberbe* woodland; K = *Grewia flava* - *Croton grattisimus* shrubland; L = *Combretum apiculatum* woodland; La = *Commiphora pyrocanthoides* subassociation; M = *Schmidtia pappophoroides* grassland; N = *Anthephora pubescens* grassland; O = *Terminalia sericea* - *Bauhinia petersiana* shrubland; P = *Terminalia sericea* - *Combretum collinum* woodland; Q = *Burkea africana* woodland; R = *Baikiaea plurijuga* woodland.

ASSOC		%CLAY	%SILT	%SAND	pH	Ca	Mg	K	Na	P	DEPTH (m)
B	x	7.6	10.6	81.6	8.5	2884.6**	150	371*	245.8**	2.0	0.63
	range	3-17	4-16	67-93	7.8-9.0	2321-3433	32-348	170-767	11-1000		0.1-1.5
	se	(5.2)	(6.3)	(10.8)	(0.4)	(462.8)	(114.5)	(268.8)	(383.6)	0	(0.54)
C	x	2.7	1.9	95.4	8.2	1867.5	63.8	87.7	6.7	5.4	0.11
	range	0-5	0-5	92-99	7.9-8.6	820-2652	22-88	24-160	2-18	2-20	0.1-0.2
	se	(1.5)	(1.5)	(2.5)	(0.2)	(692.9)	(22.0)	(48.1)	(5.4)	(6.0)	(0.03)
D	x	7.6	4.2	88.2	7.9	1870.2	128.2	166.6	5.4	6.5	0.12
	range	2-16	1-10	81-97	7.4-8.6	1083-2904	28-200	73-260	4-8	2-12	0.1-0.2
	se	(6.1)	(3.4)	(8.2)	(0.4)	(657.0)	(63.7)	(76.7)	(1.9)	(4.1)	(0.04)
E	x	5.3	3.4	91.3	7.9	2201.4	72.4	47.7**	490.9**	2.0	0.3
	range	3-7	2-5	89-93	6.8-9.0	319-7326	20-225	23-85	295-1000	0-2.5	0.2-0.5
	se	(1.2)	(1.4)	(1.5)	(0.7)	(2586.8)	(71.7)	(20.0)	(249.0)	(0.9)	(0.11)
F	x	8.4	3.7	87.8	6.8	1314.5	288.9**	65.2	185.9**	3.3	0.46
	range	3-15	1-5	80-91	5.9-8.0	483-2726	181-460	60-90	6-360	2.3-4.5	0.2-1.0
	se	(3.8)	(1.5)	(5.0)	(0.8)	(848.7)	(102.8)	(27.9)	(126.9)	(0.9)	(0.35)
G	x	5.8	3.4	90.8	7.0	1111.3	160.8	200.0	4.5	2.3	1.26
	range	1-10	2-6	86-97	5.3-8.4	86-2940	87-286	42-550	2-8	0-4.9	0.2-1.5
	se	(2.3)	(1.1)	(2.9)	(0.8)	(832.8)	(61.0)	(137.1)	(1.7)	(1.2)	(0.49)
H	x	9.0	3.1	87.9	6.6	822.2	207.5	132.4	14.6	2.2	0.7
	range	5-15	1-6	79-94	6.0-7.6	242-1872	94-396	27-328	2-50	2-3.3	0.3-1.5
	se	(3.8)	(2.1)	(5.8)	(0.6)	(545.8)	(110.2)	(98.0)	(20.1)	(0.5)	(0.5)
I	x	3.6	1.4	95.0	4.8	272.6**	78.4	90.1	2.7	3.2	1.5
	range	3-4	0-3	94-97	3.8-5.6	161-386	53-104	51-126	1-4	2-10	
	se	(0.5)	(1.1)	(1.1)	(0.5)	(82.2)	(20.9)	(27.4)	(1.1)	(3.0)	0
J	x	4.8	2.6	92.6	7.6	1207.4	107.2	91.6	2.8	3.7	0.58
	range	3-6	2-4	92-94	6.5-8.0	710-2618	43-180	35-147	2-4	2-7.1	0.1-1.0
	se	(1.3)	(0.9)	(0.9)	(0.6)	(806.5)	(54.0)	(43.2)	(0.8)	(2.0)	(0.4)
K	x	6.1	4.2	89.7	7.6	1432.2	93.5	104.5	3.1	3.0	0.41
	range	3-11	1-9	82-95	5.6-8.6	153-3478	38-173	19-200	2-9	2-10	0.1-1.2
	se	(2.3)	(2.3)	(3.6)	(0.7)	(1001.6)	(36.9)	(42.5)	(1.7)	(1.9)	(0.29)
La	x	5.5	2.8	91.6	6.8	662.2*	82.4	61.9**	3.1	2.1	0.62
	range	3-12	1-4	84-95	5.8-7.9	218-1297	45-124	26-99	2-5	2-3.3	0.1-1.5
	se	(2.5)	(1.0)	(2.8)	(0.7)	(355.4)	(23.3)	(24.6)	(1.1)	(0.4)	(0.48)
L	x	5.7	3.1	91.1	6.7	609.8*	98.6	75.2	3.7	2.0	0.8
	range	3-12	1-6	82-95	4.0-7.9	43-1376	45-275	19-275	2-7	0-5.9	0.1-1.5
	se	(2.3)	(1.3)	(3.2)	(0.8)	(386.4)	(50.0)	(48.0)	(1.3)	(1.0)	(0.53)
M	x	7.6	2.2	90.1	6.4	1073.2	176.6	79.9	4.6	2.0	1.09
	range	4-12	0-6	84-96	5.2-7.4	281-1876	63-459	29-185	2-9	0-3.3	0.3-1.5
	se	(2.1)	(1.7)	(3.0)	(0.5)	(458.5)	(109.9)	(37.3)	(2.1)	(0.6)	(0.56)
N	x	5.3	2.6	92.1	6.2	599.5**	136.5	73.6	3.2	2.0	1.5
	range	2-12	1-6	82-96	5.2-7.4	267-1232	59-309	37-131	1-6	2-2.3	
	se	(2.5)	(1.5)	(3.2)	(0.5)	(272.5)	(71.5)	(26.7)	(1.4)	(0.1)	(0)
O	x	3.5	2.1	94.6	5.4	186.0	61.7	26.0**	3.7	1.7	1.5
	range	2-7	0-6	88-97	4.0-7.3	42-522	10-205	7-102	2-5	0-2.5	
	se	(1.6)	(1.7)	(2.6)	(1.0)	(166.2)	(66.9)	(22.3)	(0.8)	(0.7)	(0)
P	x	3.3	1.8	94.8	5.7	188.3**	39.4*	28.5**	3.7	2.5	1.5
	range	2-5	1-3	92-97	4.8-7.3	56-526	22-100	11-56	1-8	0-10.5	
	se	(1.0)	(0.7)	(1.3)	(0.7)	(111.0)	(19.1)	(12.5)	(2.0)	(2.3)	(0)
Q	x	3.2	1.0	95.7	5.6	195.2**	37.5*	18.9**	4.7	2.3	1.5
	range	2-6	0-2	93-97	5.1-6.3	54-388	6-134	9-35	2-13	2-3.5	
	se	(1.3)	(0.5)	(1.4)	(0.4)	(125.2)	(41.6)	(8.2)	(3.5)	(0.6)	(0)
R	x	2.0	1.4	96.6	4.9	168.2**	27.6*	18.6**	3.4	2.2	1.5
	range	1-3	1-2	96-97	3.8-6.0	56-311	17-37	11-29	3-4	2-2.6	
	se	(0.7)	(0.5)	(0.5)	(0.8)	(93.4)	(9.0)	(7.9)	(0.5)	(0.2)	(0)

Extreme soil mineral concentrations are clearly noticeable in the table, (e.g., 490.9 μmol.gm^{-1} sodium in the *Sporobolus coromendalianus* association (B)). Most of these extreme values are difficult to relate directly to any feature of the vegetation associations, except the high sodium values recorded in the *Odyssea paucinervis* (C), *Sporobolus coromendalianus* (B) and *Sansevieria pearsonii - Croton menyhartii* (F) associations. The sodium concentrations recorded in these associations are known to be harmful to plants (Donahue *et al.*, 1983) and a degree of salinity adaptation would be required for species to survive these conditions. There can be little doubt that sodium would be an important factor in determining the floristic composition of these associations.

Harsh environmental conditions (in this case salinity), through eliminating sensitive species, are thought to give rise to species poor communities (Whittaker, 1972) and it is noticeable that all three associations are species poor (Table 3.3, page 38). For example, the *Odyssea paucinervis* (C) and *Sporobolus coromendalianus* (B) associations are dominated by a single species of grass (see Table 3.3, page 38) and the groundlayer of the *Sansevieria pearsonii - Croton menyhartii* (F) association is dominated by *S. pearsonii* to the exclusion of virtually all herbaceous species except a few succulent forbs (Table 3.3, page 38).

Other soil mineral concentrations are less easy to interpret. The absolute amounts of calcium, magnesium, potassium and phosphorus are known to be important as nutrients regulating plant growth (Donahue *et al.*, 1983; Greenland & Hayes, 1981; Tolsma *et al.*, 1987), but little is known about the importance of the ratios of these nutrients (Donahue *et al.*, 1983).

It is beyond the scope of this study to determine in detail the effects of specific soil physico-chemical parameters on vegetation distribution, composition and structure. Data were collected on the assumption that vegetation characteristics reflect the interactions of many favourable and unfavourable soil factors. The soil physico-chemical data given in Table 4.1 can be used as surrogate data for indexes of composite factors that were not calculated or measured directly. Two composite indexes useful in the analysis of the ordinational data are:

(i) Soil elements. Potassium (K), magnesium (Mg), calcium (Ca) and phosphorus (P) are macronutrients and are essential inorganic nutrients for plant growth (Raven *et al.*, 1981). Sodium (Na), while being harmful to many plant species at high concentrations is known to be required by a least some plant species that utilize the C_4 photosynthetic pathway (Raven *et al.*, 1981), the predominant photosynthetic pathway in tropical savanna systems (Tothill & Mott, 1985; Walker, 1985a; Cole, 1986). The total amount of these elements available in a soil can be used as an index of the soil nutrient status or fertility (Donahue *et al.*,1983).

(ii) Soil grade. The relative amounts of clay, silt and sand provide an index of soil water permeability and soil water retention capacity. Sandy soils have a high infiltration capacity and high permeability with low moisture holding capacity (Tinley, 1982). Clay-rich soils in contrast, are relatively impermeable and the charged clay minerals tend to bind water tightly (Donahue *et al.*, 1983). Clay soils are regarded as being relatively xeric substrates in areas of highly seasonal rainfall (Tinley, 1982).

From these indexes it may be concluded that most soils in eastern Bushmanland have low water retention capacities (most are sands) and that the soils are of low to moderate fertility. Taken further, the high mineral nutrient concentrations found in the soils of certain associations may be assumed to be of primary importance as determinants of the vegetation.

However, the indexes of soil fertility and water holding capacity are of value only as broad indexes, and reflect little of the complex manner in which soil physico-chemical properties may possibly determine the composition, structure and distribution of vegetation. For example, many plant species exhibit narrow ranges of pH tolerance (Raven *et al.*, 1981), but whether these narrow ranges are determined by pH affected nutrient availability or pH *per se* is hard to ascertain. In alkaline soils some cations are precipitated and certain elements may become unavailable to plants (Raven *et al.*, 1981). Soil acidity, on the other hand, decreases the availability of macronutrients (Ca, Mg, P) and increases the solubility of trace elements such as copper and iron (Reid & Horvath, 1980), at the same time as lowering cation exchange capacity (Donahue *et al.*, 1983).

4.3.2 *The ordinations.*

Floristic data were ordinated using detrended correspondence analysis (DCA) and the soil data ordinated using principal components analysis (PCA).

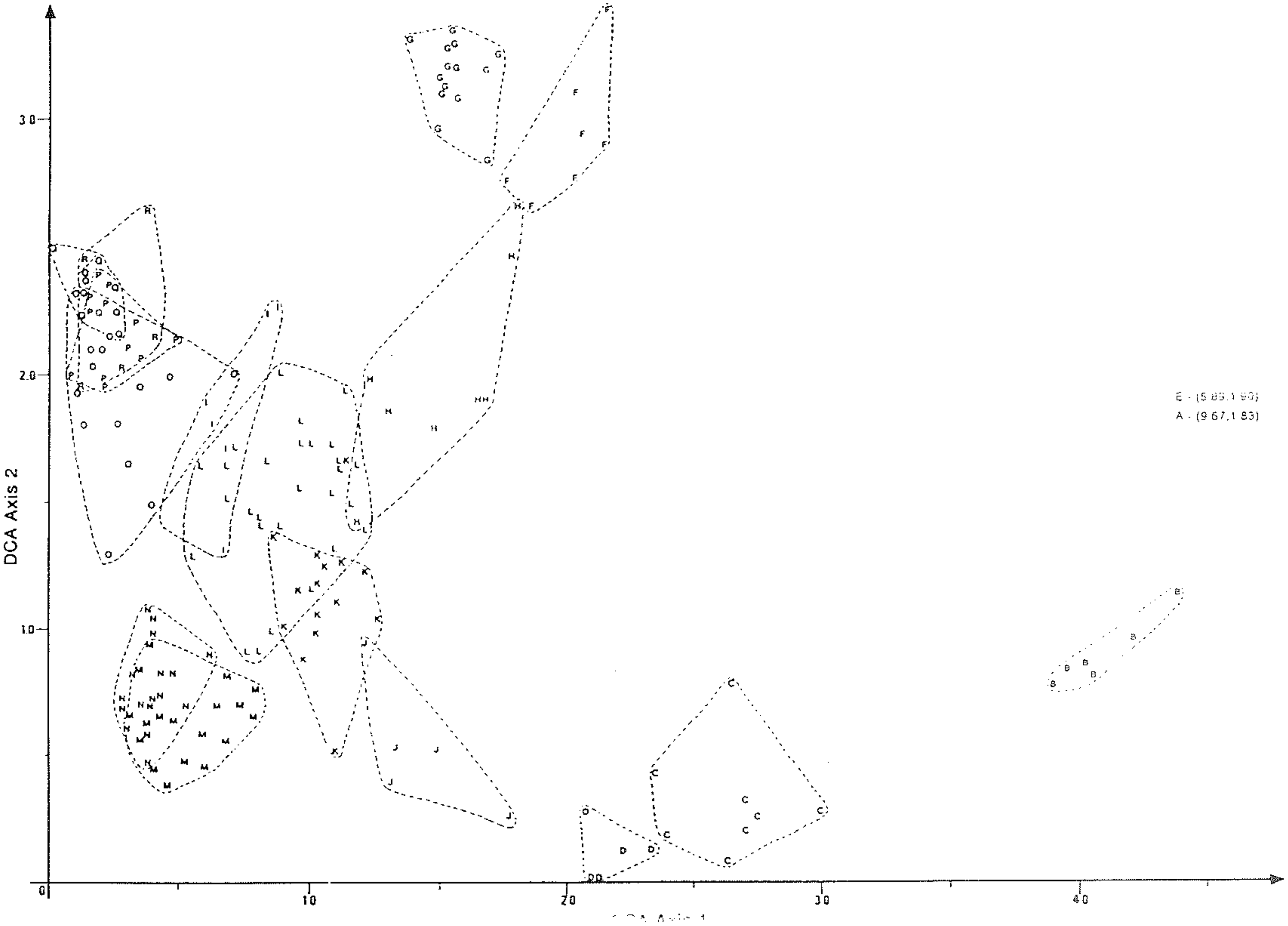
To test whether there was any correlation between the vegetation and the soil variables ordinated, a simple regression was performed. Floristic sample scores (dependant variable) from the DCA, were regressed against soil variable sample scores (independent variable) from the PCA for each sample site. This was found to be highly significant ($r = -0.84$; $p < 0.0001$). As the data in many cases are not normally distributed (several associations are undersampled and some of the data are skewed) Spearman's Rank Correlation was used to test the validity of the simple regression result using the same data. The result was found to be highly significant ($r = -0.89$; $p < 0.0001$). The high r co-efficient values indicate that in this study the underlying environmental gradients determining vegetation variation are likely to be related to changes in soil variables.

4.3.2.1 The floristic ordination.

The ordination of floristic data given by DCA is shown in Figure 4.1.

DCA produces ordinations where sample (site) and species ordinations correspond precisely, as species ordination scores are derived from averages of the sample scores and *vice versa* (Gauch, 1982). Species scores reflect individual species performance along derived environmental gradients (DCA Axes 1-4). As there is little or no information regarding habitat preferences or ecological specificity of the species, it is difficult to make inferences regarding the ordinational gradient. Sample (site) scores are however, composite performance scores of the species occurring at any one site and the ordinational gradients are easier to interpret as little information is

Figure 4.1 Scatter plot for the first two axes of DCA sample ordinations, derived from floristic data. Axis lengths are scaled in SD units (Gauch, 1982). Letters for each grouping correspond to associations described in Chapter 3, page 36-71. Key: A = *Acacia kirkii* wetland; B = *Odyssea paucinervis* grassland; C = *Acacia luederitzii* - *Combretum hereroense* woodland; D = *Combretum imberbe* - *Melinis repens* woodland; E = *Sporobolus coromendalianus* grassland; F = *Sansevieria pearsonii* - *Croton menyhardtii* thicket; G = *Terminalia prunioides* woodland; H = *Acacia erubescens* woodland; I = *Acacia erioloba* - *Eragrostis jeffreysii* woodland; J = *Cenchrus ciliaris* - *Combretum imberbe* woodland; K = *Grewia flava* - *Croton grattisimus* shrubland; L = *Combretum apiculatum* woodland; M = *Schmidtia pappophoroides* grassland; N = *Anthephora pubescens* grassland; O = *Terminalia sericea* - *Bauhinia petersiana* shrubland; P = *Terminalia sericea* - *Combretum collinum* woodland; Q = *Burkea africana* woodland; R = *Baikiaea plurijuga* woodland.


DCA Axis 2
3.0
2.0
1.0
0
10
20
30
40
DCA Axis 1
E - (5.85,1.90)
A - (9.67,1.83)
B
C
D
F
G
H
I
J
K
L
M
N
O
P
Q
R

required regarding habitat preferences of the species involved. Figure 4.1 presents the sample (site) ordinational scores only.

Two associations, the *Acacia kirkii* (A) and *Sporobolus coromendalianus* (B) associations are not shown, as they are outliers (9.6 SD and 5.9 SD units respectively) and cause the relationships of the other associations to be obscured through compaction of the graph.

Axis 1 is thought to reflect a gradient running from deep, well-drained Kalahari sand soils (0.5 SD) to poorly drained shallow soils of the Central Basin, the most extreme example being the *Acacia kirkii* association (9.6 SD) on vertic clays which are subject to flooding.

No obvious ecological or environmental explanation could be inferred from the second axis. This may be due to the high eigenvalue of the first axis (0.91) which may obscure relationships in the higher axes due to the small variance accounted for by the second and higher axes. However, the eigenvalue of Axis 2 (0.38) is not so low as to be discounted as far as interpretation is concerned. That the axis is not easily interpretable may be regarded as an indication of the importance of "noise" in the data (Gauch, 1982) and the effectiveness of the first axis in accounting for most of the initial variance in the data.

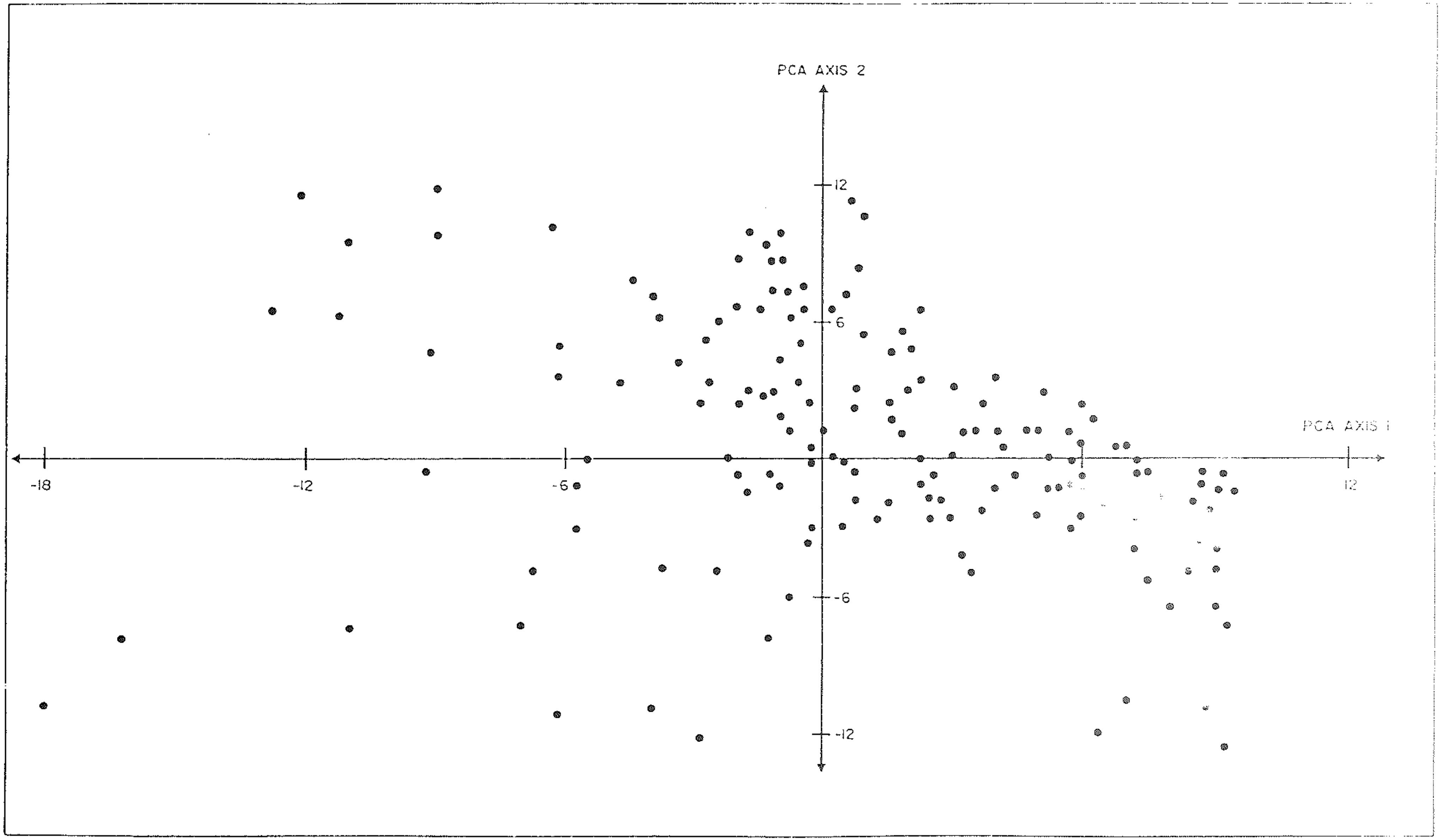
The problem of interpreting the second axis may be compounded by the clear discontinuities (e.g. the *Acacia kirkii* association (A) at 9.6 SD) in the data. DCA has been shown not to perform optimally on data with sharp discontinuities, rendering axes difficult to interpret (Moore & Chapman, 1986; ter Braak & Prentice, 1988). This problem may be overcome through the use of canonical correspondence analysis.

Canonical correspondence analysis (CCA) is an ordinational technique which has been shown to handle discontinuous data well and has gained wide acceptance in plant ecological studies in recent years (Skarpe, 1986; ter Braak & Prentice, 1988). It has, however, not been widely available in southern Africa. In CCA axes are linear combinations of environmental variables and perform as multivariate direct gradient analyses (DCA and PCA are indirect techniques) (Kent & Ballard, 1988). CCA has been shown to be effective in detecting species-environment interrelationships as well as species responses to specific environmental variables (Kent & Ballard, 1988; ter Braak & Prentice, 1988).

4.3.2.2 The soil ordinations.

Data for the ten soil variables listed in Table 4.1 were ordinated using principal components analysis (PCA). The output is shown in Figure 4.2. The first two components

Figure 4.2 Scatter plot of all PCA sample scores derived from the ordination of soil physico-chemical data for eastern Bushmanland. Twenty-five observations are hidden. Four extreme values (<-18) not shown.


PCA AXIS 2
12
6
-6
-12
PCA AXIS 1
-18
-12
-6
12

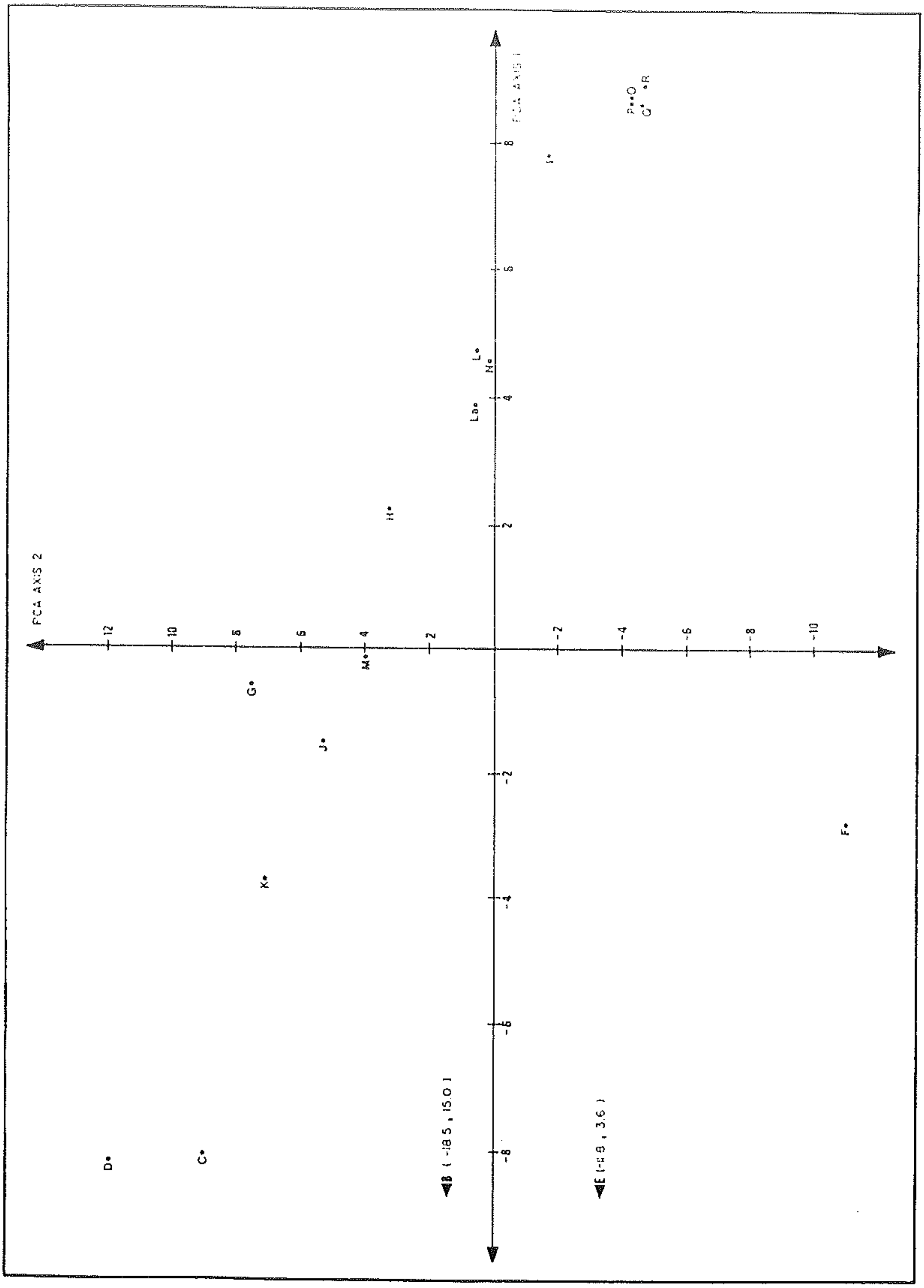
(Axis 1 & Axis 2) account for *c.* 99 % of the variation in the soil data and are therefore, considered adequate to indicate possible soil habitat gradients. Axis 1 accounts for 97 % of the variance in the data and Axis 2 only 1.7 %. These figures are high for multivariate data. They are, however, misleading as there is strong auto-correlation between certain soil variables and the percentage of clay, silt and sand, and the depth of the soil. In the sample data, the deepest soils have the lowest pH's, lowest percentages of clay and silt and the lowest overall mineral nutrient content (Table 4.1). Reciprocal changes in the percentages of sand, silt and clay (i.e. for any increase in clay content there is a decrease in sand content) in the data set are also thought to have contributed to the variance accounted for by Axis 1 in the PCA.

Although the first Axis of the PCA ordination in Figure 4.2 accounts for much of the variance in the data, the ordinational gradient is difficult to interpret and is largely obscured. The problem of interpretation lies in the number of hidden samples and the highly variable values of the soil characteristics in any given vegetation association (see Table 4.1 for ranges and standard errors). The variability of the soil characteristics in any one association shows a degree of overlap with other associations and hence no clear discontinuities between associations can be determined from the ordination shown in Figure 4.2.

In an attempt to define the ordinational gradient more clearly the PCA sample scores were grouped together according to the vegetation association into which the sample fell, and the mean value of the PCA scores for each vegetation association calculated. These mean scores were plotted on the same ordinational axes as Figure 4.2 and a clearer definition of the ordinational gradient is shown in Figure 4.3.

The distribution of the vegetation associations along the ordinational gradient derived from soil data (PCA) shown in Figure 4.3, closely parallels the distribution of associations along an ordinational gradient derived from floristic data (DCA) (Figure 4.1). The gradient shown in Figure 4.3 (and by association, Figure 4.1) is thought to represent a compound gradient of increasing soil depth, sand percentage of the soil and soil water permeability, and decreasing pH and soil mineral concentrations. This gradient may be a "complex gradient" as described by Whittaker (1971), where a number of environmental factors change together along the gradient, and all have some influence on the vegetation, but the effects of the individual factors cannot be isolated.

Figure 4.3 Scatter plot of averaged PCA sample scores grouped according to the association in which the sample site was located. Axes and sample scores derived from the ordination of soil physico-chemical data for eastern Bushmanland. Key to the associations: B = *Odyssea paucinervis* grassland; C = *Acacia luederitzii* - *Combretum hereroense* woodland; D = *Combretum imberbe* - *Melinis repens* woodland; E = *Sporobolus coromendalianus* grassland; F = *Sansevieria pearsonii* - *Croton menyhardtii* thicket; G = *Terminalia prunioides* woodland; H = *Acacia erubescens* woodland; I = *Acacia erioloba* - *Eragrostis jeffreysii* woodland; J = *Cenchrus ciliaris* - *Combretum imberbe* woodland; K = *Grewia flava* - *Croton grattisimus* shrubland; L = *Combretum apiculatum* woodland; La = *Commiphora pyrocanthoides* sub-association; M = *Schmidtia pappophoroides* grassland; N = *Anthephora pubescens* grassland; O = *Terminalia sericea* - *Bauhinia petersiana* shrubland; P = *Terminalia sericea* - *Combretum collinum* woodland; Q = *Burkea africana* woodland; R = *Baikiaea plurijuga* woodland.


PCA AXIS 1
PCA AXIS 2
12
10
8
6
4
2
-2
-4
-6
-8
-10
P
O
Q
R
I
L
N
La
H
M
G
J
K
F
D
C
B (-18.5, 15.0)
E (-19, 3.6)

4.4 DISCUSSION

The determinants of savanna structure, distribution and composition has been and remains the subject of debate (see Tothill & Mott, 1985 and Walker, 1985b for recent reviews). Most studies have demonstrated how difficult it is to assess the degree to which any one factor such as soil nutrients or sub-soil drainage conditions controls or determines savanna characteristics. McNaughton (1983) and Whittaker (1971), however, stress the importance of composite environmental factors in plant community organisation. These composite factors are implemented through many intermittent and interactive weak forces. It is generally much easier to characterise the composite factors than to identify the specific determinants of individual species or groupings.

The nature of the data ordinated here is such that only composite factors are likely to be reflected in vegetation differences. In this study it is clear that the vegetation comprises a disjunct mosaic of discontinuous associations rather than a broad continuum. As the ordination techniques employed (DCA and PCA) do not perform optimally on discontinuous data it is difficult to determine, directly from the ordinations performed, which factors are important. For this reason the importance of certain factors in determining the characteristics of vegetation types described in other studies, is used to highlight possible determinants of the vegetation associations in the present study.

4.4.1 *The determinants of the associations.*

4.4.1.1 Factors affecting associations occupying deep sand habitats.

The four associations typical of the Kalahari sand areas are *Terminalia sericea - Bauhinia petersiana* (O), *Terminalia sericea - Combretum collinum* (P), *Burkea africana* (Q) and *Baikiaea plurijuga* (R). They show broad overlaps in the floristic ordination (Figure 4.1), indicating many shared species (see also Table 3.5, page 63). The PCA ordination (Figure 4.3) and Table 4.1 show the associations as having very similar soil characteristics, the most prominent features of which are the high sand fraction of the soil, the acid pH and the low overall nutrient status of the soil.

Medina (1985) suggests that soils of low fertility select for species with low nutritional requirements or for species highly adapted to exploiting the soil nutrient resources. In nutrient-poor soils a primary response to low concentration of nutrients in the soil solution is an increased allocation of energy and resources to developing a large root system (Sarmiento *et al.*, 1985). High root:shoot biomass ratios allow an increased relative water and nutrient uptake. Rushworth (1975) studying the dynamics of woody species on Kalahari sands in Zimbabwe found that in test plots containing a number of species common to the present study, 85 % of the standing crop was below ground. Species present included *Terminalia sericea, Baikiaea plurijuga, Baphia massaiensis, Bauhinia petersiana, Combretum collinum, Pterocarpus angolensis, Lonchocarpus nelsii* and *Ochna pulchra*. This may indicate a high degree of specialised adaptation to nutrient poor conditions, and in this study it is thought that these nutrient poor conditions of the Kalahari sands determine to a large extent the species composition of the four associations.

Childes & Walker (1987), also working on Kalahari sand vegetation in Zimbabwe, found that the distribution and species composition of associations was determined in part by moisture changes in the soil profile dictated by the presence of a hard sand layer at *c.* 1.00-2.75 m. Where the hard layer was present, *B. plurijuga* was either absent or badly stunted and the vegetation was dominated by *T. sericea*. The hard sand layer was thought to impede drainage and stunt the root growth of *B. plurijuga* through temporary waterlogging.

Baikiaea plurijuga has a distinctive distribution in eastern Bushmanland, occupying the crests of large dunes and hummocks thought to be the remnants of degraded dunes.

Baikiaea plurijuga is a deep rooted (>10 m; Childes & Walker, 1987), evergreen species with synchronous leaf-drop and replacement at the end of the dry season (Childes, 1989). To maintain an evergreen habit, a species requires access to water year round (Sarmiento et al., 1985). In sandy soils, the upper levels of the soil profile dry rapidly in the dry season and only deep rooted species have access to the permanent water resources which occur at relatively deep levels (Medina, 1985; Childes & Walker, 1987). These deep sandy soil conditions are thought to occur only on the large dunes and hummocks described above; the limited distribution of *B. plurijuga* within the study area is determined largely by the distribution of the dunes and hummocks.

The *Acacia erioloba* association (I) has a distinct north-south distribution along the western margin of the study area where it occupies soils with similar characteristics to the Kalahari sand associations (O, P, Q, R) (Table 4.1, Figure 4.3) and has distinct floristic affinities with these associations (Table 3.4 & 3.5, pages 49 & 63; Figure 4.1). Soil mineral values are slightly higher in the *A. erioloba* association than those recorded in the Kalahari sand associations, but differences in vegetation characteristics are difficult to ascribe to any one soil factor.

The dominance of evergreen woody species, such as

A. erioloba and *Boscia albitrunca*, is indicative of mesic soil-water conditions (Sarmiento *et al.*, 1985). Elsewhere in the Kalahari *A. erioloba* occupies habitats with elevated water-tables (along river courses) or mesic rooting conditions (the crests of dunes and pan soils associated with depressions) (Leistner, 1967; Cole & Brown, 1976; personal observation). A number of boreholes in areas occupied by the *A. erioloba* association show relatively shallow water-tables (e.g. 12 m at CDM Camp, 11 km West of Tsumkwe). Thus the presence of a shallow water-table may be an important determinant of the *A. erioloba* association.

The two grassland associations (*Schmidtia pappophoroides* (M) and *Anthephora pubescens* (N)) have similar floristic compositions (see Table 3.5, page 63) and this is clearly reflected in Figure 4.1 where there is a broad overlap of the two associations. From this it may be inferred that the two associations have similar ecological determinants. However, the two associations are widely separated spatially in the field and soil conditions differ markedly (Table 4.1) with respect to soil depth and calcium content. This is reflected in the ordination shown in Figure 4.3. There is little difference in soil pH (Table 4.1), but the higher calcium content of the *S. pappophoroides* (M) association must determine a more base-rich soil environment. The differences (in soil depth and calcium content) may be inferred to exert some influence on the development of grasslands in eastern Bushmanland. However, interpretation of the ordinational gradient is complicated by the dominance (in both associations) of a number of species with wide ecological tolerances such as *Schmidtia pappophoroides, Brachiaria nigripedata* and *Digitaria eriantha* (Gibbs-Russell *et al.*, 1990).

A noticeable difference between the two grassland associations (M, N) is the distribution of woody species within them. In the *S. pappophoroides* association (M) woody species tend to be restricted to termitaria (Plate 3.17, page 62) and are often species commonly found on shallower soils (e.g., *Grewia flava, Combretum hereroense*). Termitaria are thought to provide a sub-habitat which allows the establishment of species not adapted to the surrounding habitat (Griffioen & O'Connor, 1990; Glover *et al.*, 1964) .

4.4.1.2 Factors affecting associations on shallow to moderately deep soils.

Localised edaphic conditions are thought to be important in determining the vegetation characteristics of the remaining associations (A - H, J - L). In Figures 4.1 and 4.3 these associations are clearly separated on the ordinational gradient, indicating few shared species and distinctly different soil characteristics. The factors thought to be most important in determining these associations are: the nature and type of sub-surface geological formations and, the presence or absence of a pan horizon in a soil, the duration of flooding and the soil salinity.

4.4.1.2.1 Sub-surface geology.

Detailed biogeochemical studies in the Kalahari of western Botswana and Namibia found in some cases that the adjustment between plant distributions and edaphic factors is so close that individual plant communities delineate the underlying geological formations (Cole & Brown, 1976; Cole & le Roux, 1978), and in some cases reflect concealed fold structures (Cole & Brown, 1976). These studies involved determining the rooting characteristics of certain common species (*Terminalia prunioides, Combretum imberbe, Grewia flava*), the mineral status of the soil and the importance of soil differences related to texture and moisture availability.

In eastern Bushmanland, sub-outcropping geological strata exert a similar effect on the vegetation. In Plate 2.2 (page 13) the large open folds in Nosib quartzites are clearly delineated by dense stands of the *Terminalia prunioides* association (G). In Plate 4.1 the fine striations are alternating narrow bands of *Combretum apiculatum* trees and *Cenchrus ciliaris* grass on bands of hard and soft dolomite. The exact determinants of the distribution of the vegetation is uncertain, but as the underlying geology and climatic conditions are similar to those described by Cole & Brown (1976), soil moisture conditions, rooting environment and mineral nutrient status are thought to be of primary importance in determining the patterns illustrated in Plate 2.2 (page 13) and Plate 4.1.

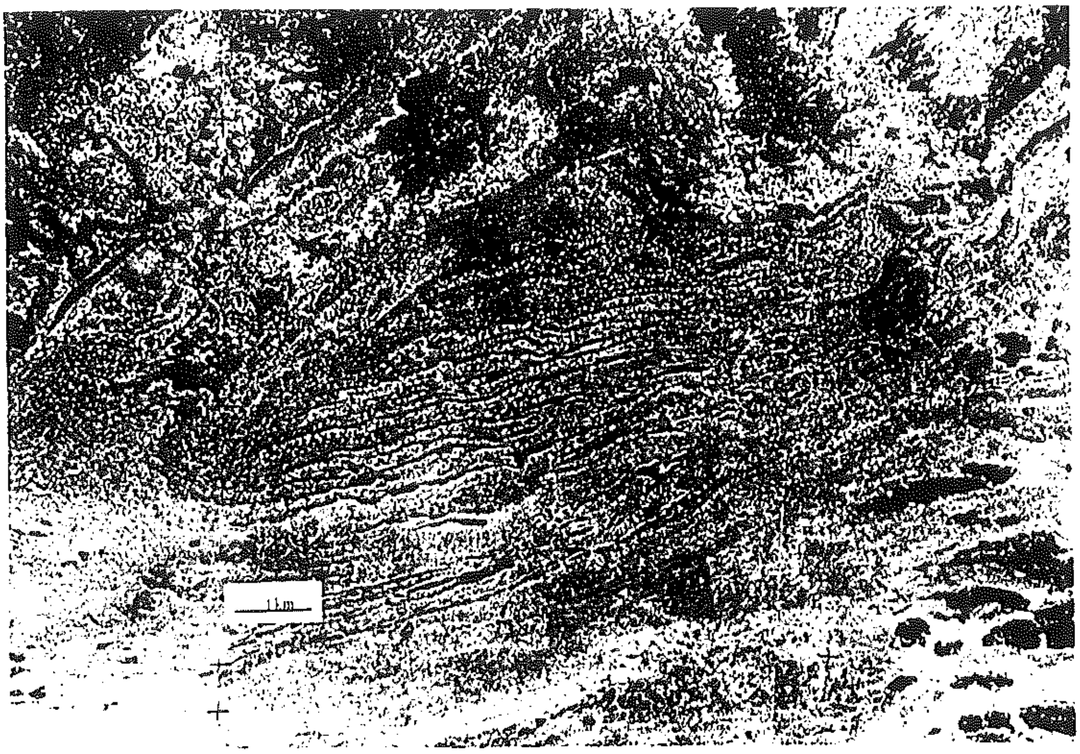


Plate 4.1. Aerial photograph of differently vegetated bands of soft and hard dolomite near the Aha Hills.

Differences in underlying geological strata are known to influence the species composition of vegetation units (Cole 1986), as parent material is important in determining the nutrient status of the overburden soils

(Donahue *et al.*, 1983; Cole, 1986; Walker, 1985b).

The *Combretum apiculatum* association (L) is widely distributed throughout the study area, largely on quartzites and on hardpan calcretes which have undergone some silicification (silcretes). The species composition of the association varies little, with the exception of the *Commiphora pyracanthoides* sub-association (Table 3.4, page 49) which is restricted in its distribution to the granitic extrusion east of Tsumkwe. The granite is covered by a veneer of redistributed Kalahari sand, as are the quartzites and silcretes described above. The soil variables shown in Table 4.1 do not differ significantly between the association and the sub-association (In Figure 4.3 the soil characteristics of the *C. pyrocanthoides* sub-association are indicated by point **La**). The differences in weathering products in the form of clay minerals derived from the basal geology may be an important factor in determining the vegetation changes described. The felspathic minerals in granites give rise to the so-called "2 + 1" clay minerals (Donahue *et al.*, 1983) which have water-binding properties quite different to the clay minerals derived from the weathering products of silcretes and quartzites ("2 + 2" clay minerals) (Donahue *et al.*, 1983). These differences in clay mineral composition are likely to affect water-retention and the nutrient status of the soils, and may affect vegetation distributions accordingly.

4.4.1.2.2 Pan horizons, termitaria, flooding and salinity.

The presence or absence of a pan horizon, the distance of the horizon from the soil surface, changes in macro- and micro-relief and salinity have also been proposed as determinants of localised edaphic variation of vegetation (Tinley, 1982).

The *Acacia erubescens* association (H) occurs on a transition zone between areas subject to regular flooding (e.g., those areas covered by the *Sporobolus coromendalianus* association (E)) and grasslands (*Schmidtia pappophoroides* association (M)). In this study, the presence of a well developed pan horizon (usually at a depth of 0.6-1.0 m) is thought to be important in determining the distribution and species composition of the *Acacia erubescens* association (H). Pan horizons are usually associated with conditions of temporary waterlogging (MacVicar *et al.*, 1977), which are known to affect the rooting environment of plants (Cole, 1986; Childes & Walker, 1987). It is noticeable in this association that a number of woody species (e.g., *Grewia flavescens, G.bicolor, Croton grattisimus*) normally associated with drier habitats (personal observation) are found only on termitaria. The termitaria are thought to provide a xeric sub-habitat (Griffioen & O'Connor, 1990) and allow the establishment of species which otherwise would have been excluded. *Combretum imberbe*, a species tolerant of waterlogged conditions (Coates-Palgrave, 1977), is common in the association and is not associated with termitaria.

The *Sporobolus coromendalianus* (E) and *Sansevieria pearsonii* - *Croton menyhartii* (F) associations interdigitate extensively (Plate 3.5, page 63). It is conspicuous that there are no woody species in the *S. coromendalianus* association (E). The presence of a hard pan layer, large termitaria, regular flooding and saline soil conditions determine the distribution and composition of these two associations. In the *S. coromendalianus* association (E) a hard pan layer at a depth of *c.* 0.3 m, high sodium values (490 μmol.gm^{-1}, Table 4.1) and regular seasonal floods all contribute to the development of this species-poor association. The *S. pearsonii* - *C. menyhartii* association (F) is restricted in its distribution to large termitaria within the flats covered by the *S. coromendalianus* association (E). These termitaria provide ameliorating soil conditions (deeper soils, lower sodium values and no flooding), allowing a number of woody species (*Terminalia prunioides, Croton menyhartii, Albizia harveyii*) to become established in an otherwise unsuitable area.

The Nyae-Nyae area of eastern Bushmanland has a shallow mantle of soil (see Table 4.1, associations B, C, D) underlain by massive pedogenic hardpan calcrete (Netterburg, 1980). The *Odyssea paucinervis* (B), *Acacia luederitzii - Combretum hereroense* (C) and *C. imberbe - Melinis repens* (D) associations show little or no species overlap (Table 3.3, page 38; Figure 4.1) even though they are closely associated spatially. The ordination of soil variables (Figure 4.3) shows markedly different soil conditions between these associations (see also Table 4.1).

The *O. paucinervis* association (B) is found on lunette dunes and other calcareous sand deposits which develop on the lee shores of large pans and depressions in the Nyae-Nyae pan area. The high sodium values are thought to preclude all but highly saline-adapted species from this habitat.

Spatially, the *A. luederitzii - C. hereroense* (C) and *C. imberbe - M. repens* (D) associations interdigitate widely in the Nyae-Nyae area and the period of inundation to which each association is subjected is probably the most important factor in determining the distribution of these associations. The Nyae-Nyae area is periodically subjected to prolonged flooding (up to nine months; Hines, in press) and factors affecting the duration of inundation such as micro-relief features, depth of soils and the structure of the underlying calcretes are thought to be important in determining plant distributions. The

The dwarfing of the trees is thought to be caused by the massive unfractured hardpan calcretes restricting the rooting environment (Plate 4.3 & 4.4) of species that are normally deep rooted (Cole & Brown, 1976).

Plate 4.3. In the Nyae-Nyae area massive hardpan calcrete restricts root growth which is often surficial. Most of the roots of this *Combretum imberbe* are surficial.

The *Acacia kirkii* wetland association (A) is found in depressions associated with fractures in the granite outcroppings east of Tsumkwe (Figure 2.4, page 15; Plate 2.1, page 13). These depressions are clay rich, often showing vertic characteristics. The clay-rich substratum and the duration of flooding (up to 12 months (Hines, in

A. luederitzii - C. hereroense association (C) occupies well drained, elevated sites in contrast to the *C. imberbe - M. repens* association (D) which is restricted to shallow depressions and pan margins usually subject to prolonged periods of inundation (Hines, in press).

A noticeable feature of the *A. luederitzii - C. hereroense* association (C) is the dwarfed nature of the tree species (Plate 4.2). *Acacia luederitzii, C. hereroense* and *C. imberbe* are usually less than three metres tall and seldom reach greater than five metres in height.

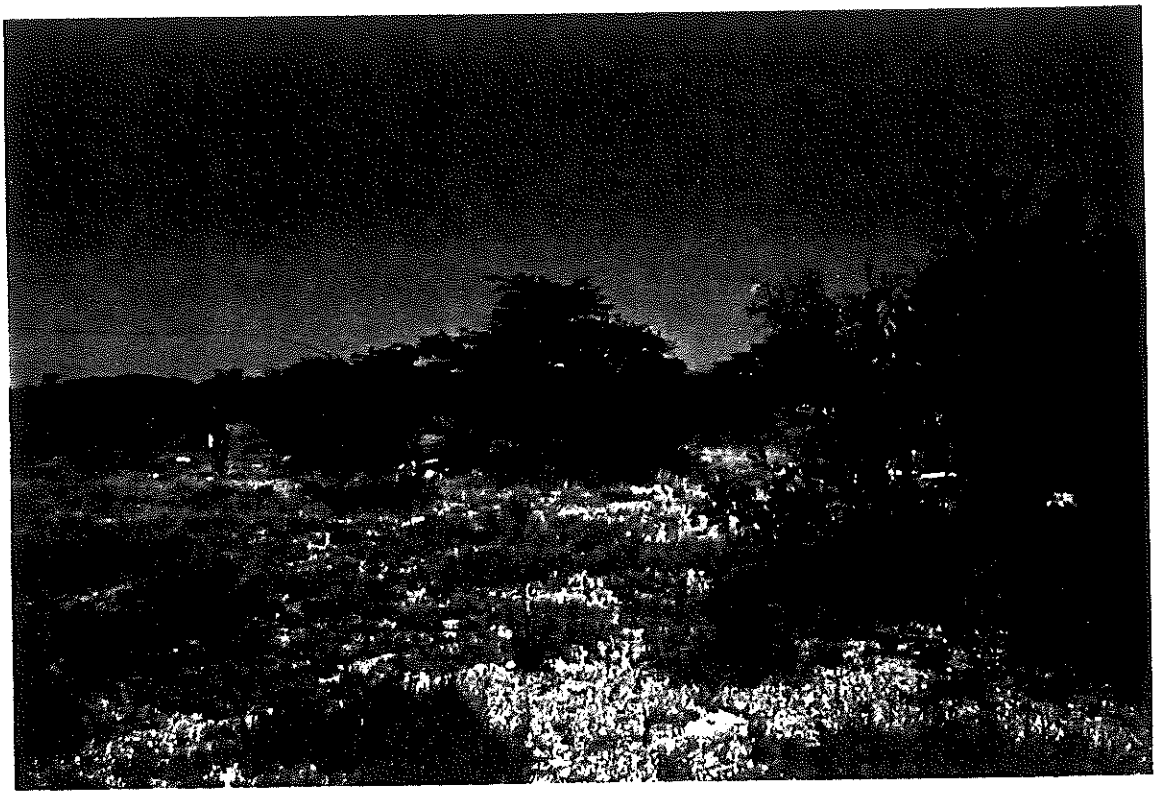


Plate 4.2. In the Nyae-Nyae area tree species are generally dwarfed seldom growing taller than five metres.

press) are thought to be important factors determining the species composition of this association.

Plate 4.4. In the Nyae-Nyae area, where the rooting environment of tree species is restricted, individuals are often blown over by strong winds. Note the very small roots of this *Acacia luederitzii*.

The factors determining the distribution, composition and structure of the *Cenchrus ciliaris - Combretum imberbe* (J) and *Grewia flava - Croton grattisimus* (K) associations are difficult to interpret from the ordinations (Figures 4.1 and 4.3) or the soils data collected (Table 4.1). Both associations are distributed on calcrete ridges and hummocks which show sharply discontinuous distributions throughout the study area. The problem of interpreting the determinants of these associations may be associated with the poor way in which PCA and DCA handle discontinuous data (ter Braak & Prentice, 1988).

4.4.1.3 The role of short term modifiers in determining vegetation characteristics.

Fire and herbivores are the two most important short term modifiers (termed "variable determinants" by Walker, 1985a) affecting vegetation characteristics in savannas. The effects of fire and herbivory were not specifically investigated in this study. Other studies in semi-arid savannas are used to highlight the possible importance of these two factors in determining vegetation characteristics in eastern Bushmanland.

Fire is known to be an important determinant of vegetation structure in *Baikiaea plurijuga* woodlands in Zimbabwe (Childes & Walker, 1987). Regular fires cause mortalities of mature trees and suppress recruitment. Initial investigations in eastern Bushmanland showed that many mature trees in the *Burkea africana* (Q) and *Terminalia sericea - Combretum collinum* (P) associations showed considerable fire damage and many saplings were reduced to coppice growth between fires (Plate 4.5).

Plate 4.5. An area of heavily burned *Burkea africana* woodland in north-eastern Bushmanland. Note the number of large dead trees (all *B. africana)* and the coppice growth of *Terminalia sericea, Bauhinia petersiana* and *Baphia massaiensis*.

The grasslands (*Schmidtia pappophoroides* (M) and *Anthephora pubescens* (N) associations) of eastern Bushmanland are regarded by Strohbach (1991) as being maintained by fire, and "regular" fires (no periodicity given) are recommended as a management action. However, it should be stressed that the role of fire in semi-arid savanna grasslands is equivocal. The return frequency of natural fires in these areas is low (up to 20 years between fires (Walker, 1985b)). Fires set by humans have decreased the interval between fires and this has been shown to have deleterious effects in other studies

(Walker, 1985b; Trollope, 1982; Frost & Robertson, 1985; Skarpe, 1980 & 1990a). Walker (1985b) contends that the vigour of the grass cover is reduced by regular fires and by subsequent grazing pressures during the dry season. Other studies (Trollope, 1982; Frost & Robertson, 1985) indicate that palatable perennials are replaced by annual forbs and grasses if burning takes place in the late wet season or early dry season, a time in which many fires are noted in eastern Bushmanland. The response of the vegetation of eastern Bushmanland to fire or protection from fire warrants fuller investigation.

The importance of herbivores in determining vegetation characteristics is the subject of a number of reviews (van Vegten, 1983; Walker, 1985b; Ruess, 1985; Tolsma *et al.*, 1987; Skarpe, 1983a). Although arthropods are significant herbivores in savanna systems (Arshad, 1982; Beckmann, 1987), Walker (1985b) contends that they are not a major determinant of savannas.

The role that herbivory has played in eastern Bushmanland in developing the vegetation characteristics present today is uncertain, but is likely to be slight. Vertebrate herbivore densities have, until recently, been low and the effects of herbivores consequently unimportant. Recent introductions (in the last ten years) of significant numbers of cattle, and the development of artificial waterholes in the area, have led to changes in grazing pressures which have resulted in marked vegetation changes. For example, Strohbach (1991) has shown an increase in bush encroachment associated with a distinct grazing gradient around an artificial waterhole (Gautscha). Where grazing pressures were highest (nearest the waterhole) there were increased numbers of known encroaching species of woody plants (*Dichrostachys cinerea, Maytenus senegalensis, Grewia flava*). These findings are similar to those of Tolsma *et al.* (1987) who studied woody plant densities around artificial waterholes in Botswana.

That certain associations (in this case the *Grewia flava - Croton gratissimus* association (K)) are subject to bush encroachment occasioned by overgrazing (Strohbach, 1991) is an important management consideration.

4.4.2 *A model of vegetation determinants in eastern Bushmanland.*

The possible determinants of the vegetation in eastern Bushmanland are similar to those recorded in other studies of savanna systems. The ordination of floristic and soils data in this study shows a close relationship between the expression of vegetation characteristics (distribution, composition and structure) and the geomorphology, soil physico-chemical environment and localised influences such as termitaria. Assuming that the close relationship between vegetation units and soil factors postulated by Cole (1982 & 1986) is relevant to this study, it is possible to construct a general model of vegetation determinants in eastern Bushmanland, based on groups of determinants at three hierarchical levels. The model is outlined in Table 4.2 and the determinants at the different hierarchical levels are explained more fully below:

> LEVEL I. Regional influences. The major division in the distribution of vegetation structural types (e.g. woodland, wetland, grassland, shrubland) is the result of factors related to climatic changes that influenced landscape evolution on a geological time scale. The palaeowinds of the Caenozoic transported sand into the area and there are now major deposits of aeolian sands within the study area. The Aha Hills acting as a barrier protected the Central Basin area from the deposition of sand (Ward & Swart, 1989) while at the same time the winds had a deflationary erosional effect on areas in the Central Basin. This has given rise to two distinct divisions in the vegetation of the study area: (i) those vegetation types occupying deep aeolian sand deposits and, (ii) those types occupying the shallower soils of the Central Basin in the lee of the Aha Hills.

Table 4.2 Simple hierarchical model of determinants of vegetation characteristics in savannas. Details of the model, relevant to eastern Bushmanland, are given on pages 122 & 124.

LEVEL	DETERMINANT/PROCESS	EFFECT/RESULT
I REGIONAL INFLUENCES	Basement geology, climatic/geomorphological/geological influences on the landscape	Determines - Vegetation Type: Woodland Shrubland Grassland Wetland
II SOIL PHYSICO-CHEMICAL INFLUENCES	Soil texture; Water retention capacity; Gross nutrient composition; Hardpan layer	Determines - Distribution, structure & composition of vegetation associations
III LOCALISED INFLUENCES	Elemental nutrient status; flooding; termitaria	Determines - Individual species distributions and structure.

LEVEL II. Soil physico-chemical influences. Within the two broad divisions described in Level I soil physico-chemical influences related to soil texture, gross nutrient composition, water retention capacity, the presence or absence of a hard pan layer, the period of inundation and the weathering products of basement geology, determine to a large extent the distribution, structure and composition of the vegetation associations found within the study area.

LEVEL III. Localised influences. This level accounts for determinants of within-association differences in species composition and structure. The presence of termitaria, fractures in basement rock, localised nutrient deficiencies and excesses, and flooding are important at this level.

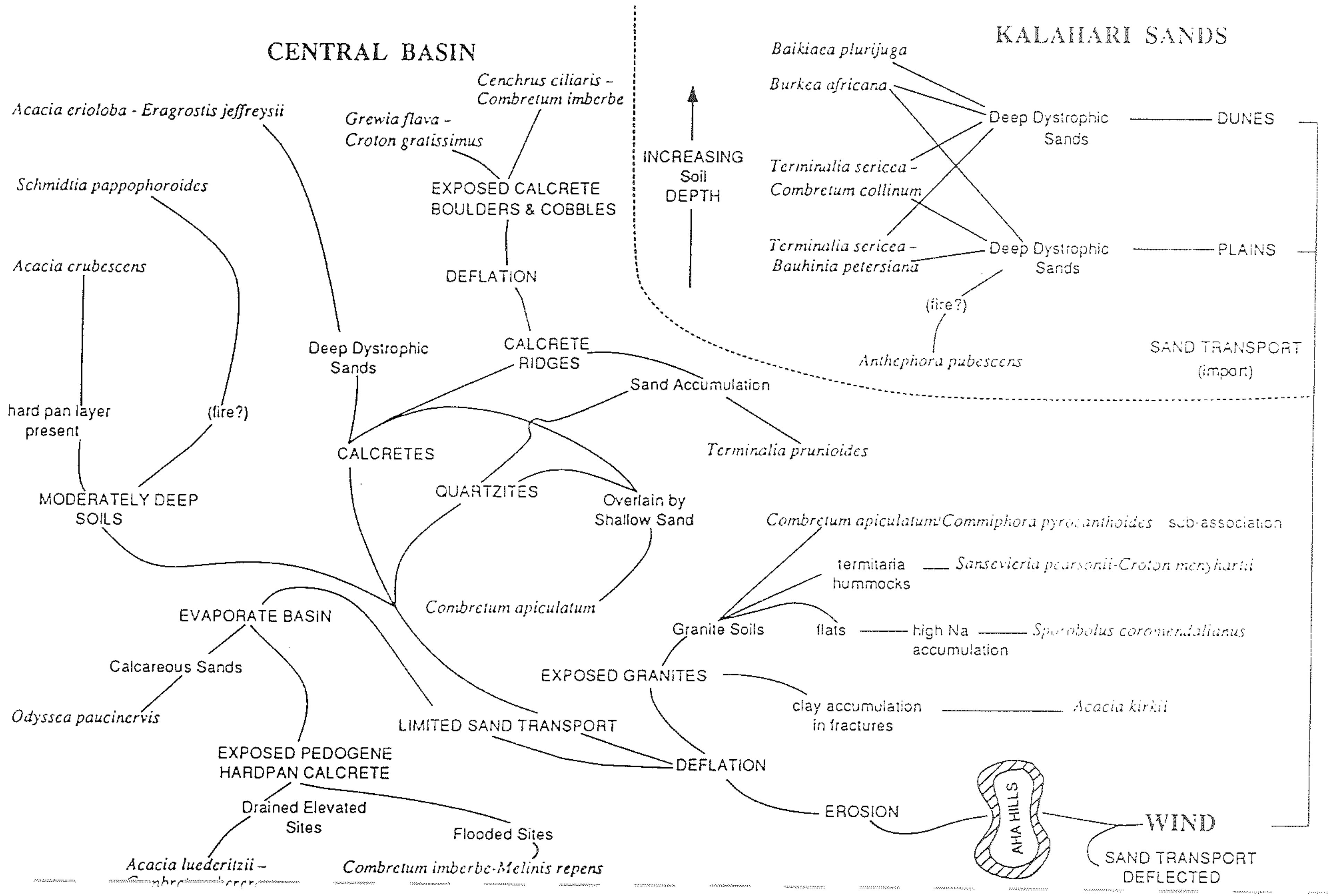
The model can be expanded further to reflect the interactions of the determinants at the three hierarchical levels in relation to the vegetation associations described and discussed above. The expanded model is shown in Figure 4.4.

The model reflects the primary environmental factors of geology, topography and climate that determine the context in which soil formation and vegetation development combine to define the savanna structure and patterns present today.

The model is essentially static as it is based on the results of data analyses not designed to reflect dynamic changes (point data rather than time-series data). The model does, however, contain dynamic elements. Changes in the geology, geomorphology and climate occur on a time scale of hundreds to thousands of years but the rates of change of some of these processes can be enhanced or retarded by the activities of man, for example erosion rates. This directly affects how savanna lands are managed.

On a management level, the model is too simplistic as it does not adequately reflect the influence of the combined set of environmental modifiers (fire, herbivory, competition, etc.) that interact with varying intensity to give rise to short term change. The relative importance of these modifiers in determining vegetation characteristics in the study area is difficult to define. Successional pathways and the direction of vegetation changes remain obscured, and inferences made from other studies may not be helpful in elucidating these pathways. For example, frequent fires and the exclusion of fires cause changes in species abundance and diversity (Childes & Walker, 1987; Sweet, 1982; Frost & Robertson, 1985).

Figure 4.4 An expanded model of the environmental determinants (outlined in Table 4.4) of the vegetation associations in eastern Bushmanland. LEVEL I determinants - Regional influences, indicated in capitals; LEVEL II determinants - Soil physico-chemical influences, indicated in upper and lower case; LEVEL III determinants - Localised influences, indicated in lower case only.


CENTRAL BASIN
KALAHARI SANDS
Baikiaea plurijuga
Burkea africana
Deep Dystrophic Sands
DUNES
Terminalia sericea - Combretum collinum
Terminalia sericea - Bauhinia petersiana
Deep Dystrophic Sands
PLAINS
(fire?)
Anthephora pubescens
SAND TRANSPORT (import)
INCREASING Soil DEPTH
Acacia erioloba - Eragrostis jeffreysii
Grewia flava - Croton gratissimus
Cenchrus ciliaris - Combretum imberbe
EXPOSED CALCRETE BOULDERS & COBBLES
Schmidtia pappophoroides
Acacia erubescens
DEFLATION
CALCRETE RIDGES
Deep Dystrophic Sands
Sand Accumulation
Terminalia prunioides
hard pan layer present
(fire?)
CALCRETES
QUARTZITES
Overlain by Shallow Sand
MODERATELY DEEP SOILS
Combretum apiculatum
Combretum apiculatum/Commiphora pyracanthoides sub-association
termitaria hummocks
Sansevieria pearsonii-Croton menyhartii
Granite Soils
flats
high Na accumulation
Sporobolus coromandelianus
EVAPORATE BASIN
Calcareous Sands
Odyssea paucinervis
EXPOSED GRANITES
clay accumulation in fractures
Acacia kirkii
LIMITED SAND TRANSPORT
EXPOSED PEDOGENE HARDPAN CALCRETE
DEFLATION
EROSION
AHA HILLS
WIND
SAND TRANSPORT DEFLECTED
Drained Elevated Sites
Flooded Sites
Acacia luederitzii –
Combretum imberbe-Melinis repens

The use of floristic and soils data to derive a simple model of savanna dynamics is justified. The primary determinants of vegetation expression are clearly elucidated and the model can be used to form the basis for a programme of management orientated research.

4.5 CONCLUSION

The semi-arid savannas of southern Africa have long been recognised as important grazing lands (Barnes, 1979; Skarpe, 1983a; Veenendal & Opschoor, 1986) and a clearer understanding of the overall determinants of the component vegetation is essential to long-term management of this resource. Coles' (1986) hypothesis, relating changes in vegetation characteristics such as structure, distribution and composition to changes in climate, geomorphology, geology and soils, provides a useful framework in which to assess the relative importance of any one environmental determinant in shaping the vegetation of an area.

Despite the limited nature of the data collected in this study, the environmental gradients influencing the distribution of vegetation associations in eastern Bushmanland, are discernable from the analysis of both the floristic and soils data. Identified gradients are relatively simple in their structure due to the degree of autocorrelation between variables in the soils. The clear differentiation of the vegetation associations based on floristic data reflects this. The influence of climatic and geomorphological history is difficult to assess, beyond broad generalities. However, the importance of the geological substrate and type of overburden, in influencing soil moisture conditions, soil nutrient status and drainage, is clearly illustrated in this study.

The interpretation of the ordinational axes and hence, the interpretation of the possible vegetation determinants could be greatly improved by the use of ordinational techniques which are robust in their handling of disjunct/discontinuous floristic and environmental data.

The importance of short term modifiers, such as fire and herbivory, in determining the vegetation characteristics was not investigated in this study. These aspects require detailed studies on their own. Lack of data regarding short term modifiers renders the model proposed inadequate on a management level.

Initial studies in eastern Bushmanland, have shown low carrying capacities for most of the vegetation associations (14-28 ha per large stock unit (Beytell, 1982; Anon., 1988). Other studies investigating grazing pressures around settlements have shown bush encroachment as a result of overgrazing (Strohbach, 1991). These aspects (low carrying capacities and bush encroachment) indicate a limited vegetation resource base requiring careful management, which is further complicated by the fragmented nature of the vegetation associations. The division of eastern Bushmanland into viable management units is likely to be problematic.

The economic viability of any development planned for eastern Bushmanland is inextricably linked to the careful management and maintenance of the vegetation resources. The following chapter reviews the priorities for research and management in eastern Bushmanland, given the need to develop a local economy based on the utilisation of the vegetation resources in the area.

CHAPTER 5

GENERAL CONCLUSIONS AND RECOMMENDATIONS FOR RESEARCH

5.1. GENERAL CONCLUSIONS

The study area falls within the Kalahari System (Cooke, 1964), a region noted for it's harsh environmental conditions and largely uniform cover of aeolian sands. Eastern Bushmanland is, however, unusual within the Kalahari System in that the mantle of sand is relatively thin. This arose as a consequence of the Aha Hills acting as a barrier to sand import into the area during the Caenozoic. The resultant exposure of bedrock geology and localised geomorphological features (dunes, pans, drainage lines, fractured rock plates) has given rise to a diversity of habitats within a limited area, which is atypical of the Kalahari System. The mosaic of vegetation units and the diversity of the flora reflects the variety of habitats within the area.

Eighteen vegetation associations were identified in the study area, each with a distinct floristic composition easily recognisable in the field. The associations compare closely with vegetation units described from other studies in southern Africa. No species or associations were restricted to the study area with the majority being widely distributed within southern Africa and many occurring beyond the boundaries of the Kalahari System itself. However, the combined assemblage of species and associations is unique within the Kalahari System and showed greater species richness and diversity of associations than areas of comparable size within the Kalahari. The uniqueness and species richness of the area gives eastern Bushmanland a high conservation priority according to guidelines established by the IUCN (1980). The vegetation associations were shown to have strong phytochorological affinities with the Zambezian Domain of the Sudano-Zambezian Region, and the exclusion of the study area from this domain by White (1983) is debatable.

From the classification of the floristic data it was clear that the vegetation formed a complex mosaic reflecting species responses to the underlying small scale pattern of geology and geomorphology. The ordination of the floristic and soils data collected confirmed the spatial pattern of small units. The environmental gradients influencing the composition, structure and distribution are discernable from the ordination of both the floristic and soils data, despite the limitations of the ordination techniques used. Findings from other studies in southern Africa proved useful in clarifying the possible determinants. Using Cole's hypothesis (1982 & 1986) that vegetation reflects the variability in habitat factors closely, a generalised model of vegetation determinants in eastern Bushmanland was constructed. Although the model does not reflect the importance of short term modifiers, such as fire and herbivory, it is useful in elucidating the possible relationships between associations and provides a framework for further research into the dynamics of successional pathways and the role of short term modifiers as determinants of vegetation in eastern Bushmanland.

Development options in eastern Bushmanland are limited. The harsh climatic conditions preclude dryland cropping as an economic venture, and so development is largely limited to the use of the vegetation as a grazing resource. In this sense there are two options, the development of a domestic livestock industry or the development and utilisation of the wildlife resources in the area. Whichever option is chosen, development and management of an economically viable undertaking is likely to be complex and problematic. Child *et al.* (1984) summarise this complex of problems thus:

> "In semi-arid rangelands economic output represents secondary biological production (i.e. animal products). It, therefore, depends directly on primary production (i.e. plant growth), but the problem is that enterprises are often not viable at

> sustainable stocking rates, so these easily damaged ecosystems are overgrazed. By over extracting environmental capital in this manner, the venture may survive in the short term, but the productivity of the ecosystem is reduced and the system is not sustainable."

The previous two chapters have shown that the vegetation of eastern Bushmanland, although possibly unique within the Kalahari System, is typical of semi-arid savannas in southern Africa in species composition, structure and environmental determinants. Studies in eastern Bushmanland (Beytell, 1982; Anon, 1988) have shown low carrying capacities for most of the vegetation associations and these are consistent with other studies in the Kalahari System (Jankowitz & van Rensburg, 1985; Skarpe, 1983b; Versveld, 1986). Bush encroachment of overgrazed areas is an additional problem in semi-arid regions (Anon, 1986; Tolsma *et al.*, 1987; Strohbach, 1990; Skarpe, 1990b). Superimposed on the complex small-scale mosaic of vegetation associations of low carrying capacities, is the high degree of spatial and temporal variability of rainfall. Resources are essentially "patchy" and the delineation of viable management units in the area is likely to be problematic.

Clearly the economic viability of any development planned for eastern Bushmanland is inextricably linked to the careful management and maintenance of the vegetation resources.

5.2 DIRECTIONS FOR FUTURE RESEARCH

The current study provides a sound base for further investigations into the plant ecology of eastern Bushmanland. Future research should focus primarily on the maintenance of the grazing resources of the area, as these underlie the ultimate success or failure of any development programme in the area. However, certain aspects of the plant ecology of the area need to be investigated before management related research programmes are instituted. These would include:

1. *Delineation of the "ecological system" investigated.*
   This study provided information on the vegetation associations and their possible determinants in eastern Bushmanland. The study area was, however, delimited along political boundaries of no ecological relevance. Eastern Bushmanland, is unusual within the Kalahari System as a whole and there is a need to define the extent of the "ecological system" studied and to place this "system" in a broader regional context more meaningful at a management level. This is required in order to define the scale of appropriate units for management and to assess the applicability of the findings of the current study to other areas within the region.

2. *The plant ecology of western Bushmanland.* The political delimitation of districts within Namibia, determines that land-use planning will be done for the whole of Bushmanland and not just for the east portion covered in this study. There is a need for information on the vegetation resources of western Bushmanland, and area predominantly covered by deep aeolian Kalahari sands. A research project similar to the present study, investigating the composition, structure and distribution of the vegetation associations and their possible environmental determinants would be required. This would provide detailed information on the possible determinants and dynamics of vegetation occurring on Kalahari sands.

3. *Phytochorological affinities of the region.* The studies proposed above would provide data for the further investigation and clarification of the phytochorological affinities of the vegetation of the region.

In eastern Bushmanland access to water determines to a large extent the patterns of land-use and settlement, wildlife concentrations and dispersal. Development scenarios proposed for eastern Bushmanland project significant increases in herbivore numbers (domestic and/or wildlife) and these populations have to be supported by the provision of artificial water points. As Tolsma *et al.* (1987) have shown in Botswana artificial waterpoints are the foci for overgrazing, bush encroachment and disturbance. This has implications for Bushmanland, where management decisions are already complicated by the fragmented nature of the vegetation pattern in the "Central Basin" and the relatively homogenous vegetation cover on the "Kalahari Sand" area. In these two areas, the differing scales of pattern in the vegetation determine that they have been settled, utilised and managed differently. In order to ensure long term sustainable utilisation of the vegetation of these areas, an appropriate scale of management unit needs to be determined in relation to the potential of the different areas to support, (i) a wildlife based economy, and/or (ii) a livestock enterprise, while at the same time maintaining ecosystem functions. Management related research should, therefore, investigate:

4. *The carrying capacities of the vegetation associations.*

   It would be necessary to determine the carrying capacities of the vegetation association, such that realistic stocking projections can be made for different species of wildlife as well as increases in domestic livestock numbers. Carrying capacities should be determined for cattle, a multispecies system (cattle and wildlife) and for wildlife only scenarios.

5. *The susceptibility of the vegetation associations to bush encroachment.*

Initial investigations by Strohbach (1991) indicated that certain associations are susceptible to bush encroachment in response to heavy grazing pressures. Information on the susceptibility of the different associations and their carrying capacities would provide important insights into placement of new waterpoints and settlements. Data on the dynamics of bush encroachment would help clarify the possible successional sequence of the different associations.

6. *The role of fire in determining the characteristics of the vegetation associations.*

Changes in fire use practices have taken place since the advent of central government control of Bushmanland. Historically the Ju/'hoansi bushmen used fire in a limited and well defined way (Marshall, 1976) much like the aboriginal people of Australia (Griffin & Friedel, 1985). These practices have largely fallen away and have been replaced by indiscriminate setting of fire at all times of the year. Current practices are likely to have serious negative effects on the grazing resources of the area. A further concern is the high frequency of fires (annual) in the western section of Bushmanland.

This has led to a serious decline in the quantity and recruitment of valuable timber trees, such as *Pterocarpus angolensis* (Cumming, 1989). Research into the response of the vegetation associations to different intervals of burning would provide information required to develop realistic policies and practices relevant to the use of fire as a management tool.

7. *The development of a dynamic model of vegetation determinants.*

Integration of the findings of research on carrying capacities, bush encroachment dynamics, the response of the vegetation to fire and the extent of system, with the findings of the present study would provide the basis of a dynamic model of vegetation determinants and succession pathways. This type of model would be far more useful at a management level than the model proposed in this study, as it would reflect the role of the short term modifiers (fire, grazing pressures) in determining vegetation characteristics.

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APPENDIX 1

A list of plant species recorded in the study area between November 1984 and May 1989.

The arrangement of families and genera, species nomenclature and authority follow Merxmuller (1972-1976) and Gibbs-Russel *et al.* (1985 & 1987), except for the Family Poaceae which follows Gibbs-Russel *et al.* 1990.

All identifications were done by the staff of the National Herbarium, Windhoek (WIND).

PTERIDOPHYTA

Family: **MARSILEACEAE**
Marsilea unicornis Launert

ANGIOSPERMAE

MONOCOTYLEDONAE

Family: **TYPHACEAE**
Typha capensis (Rohrb.) N.E. Br.

Family: **APONOGETONACEAE**
Aponogeton desertorum Zeyh. ex Spreng. fil.

Family: **HYDROCHARITACEAE**
Ottelia kunenensis (Guerke) Dandy

Family: **POACEAE**
Hemarthria altissima (Poiret) Stapf & C.E. Hubb.
Elionurus muticus (Spreng.) Kunth
Imperata cylindrica (L.) Raeuschel
Bothriochloa radicans (Lehm.) A. Camus
Schizachyrium semiberbe Nees
Andropogon gayanus Kunth var. *polycladus* (Hack.) Clayton
Andropogon schirensis Hochst. ex A. Richard
Cymbopogon caesius (Hook. & Arn.) Stapf
Cymbopogon excavatus (Hochst.) Stapf ex Burtt Davy
Hyperthelia dissoluta (Nees & Steud.) Clayton
Heteropogon contortus (L.) Beauv. ex Roem. & Schult.
Megaloprotachne albescens C.E. Hubb.
Digitaria eriantha Steud.
Digitaria gazensis Rendle
Digitaria milanjiana (Rendle) Stapf
Digitaria perrottetii (Kunth) Stapf
Digitaria seriata Stapf
Digitaria velutina (Forssk.) Beauv.
Eriochloa fatmensis (Hochst. & Steud.) Clayton
Brachiaria brizantha (Hochst. ex A. Rich.) Stapf
Brachiaria deflexa (Schumach.) C.E. Hubb. ex Robyns
Brachiaria nigropedata (Fical. & Hiern) Stapf
Brachiaria xantholeuca (Hack.) Stapf
Urochloa brachyura (Hack.) Stapf
Urochloa oligotricha (Fig. & De Not) Henr.
Urochloa trichopus (Hochst.) Stapf
Echinochloa colona (L.) Link.
Echinochloa holubii (Stapf) Stapf
Echinochloa stagnina (Retz.) Beauv.
Oryzidium barnardii C.E. Hubb. & Schweick.
Panicum coloratum L.
Panicum fluviicola Steud.

Panicum gilvum Launert
Panicum impeditum Launnert
Panicum kalaharense Mez
Panicum lanipes Mez
Panicum maximum Jacq.
Panicum schinzii Hack.
Panicum stapfianum Fourc.
Panicum trichonode Launert & Renvoize
Setaria pallide-fusca (Schumach.) Stapf & C.E. Hubb.
Setaria sagittifolia (A. Rich.) Walp.
Setaria verticillata (L.) Beauv.
Tricholaena monachne (Trin.) Stapf & C.E. Hubb.
Melinis repens (Willd.) Zizka subsp. *repens*
Anthephora pubescens Nees
Anthephora schinzii Hack.
Cenchrus ciliaris L.
Stipagrostis hirtigluma (Trin. & Rupr.) De Winter subsp. *patula* (Hack.) De Winter
Stipagrostis uniplumis (Licht.) De Winter var. *uniplumis*
Aristida adscensionis L.
Aristida congesta Roem. & Schult.
Aristida effusa Henr.
Aristida hordeacea Kunth
Aristida meridionalis Henr.
Aristida pilgeri Henr.
Aristida rhiniochloa Hochst.
Aristida scabrivalvis Hack.
Aristida stipitata Hack. subsp. *stipitata*
Aristida stipitata Hack. subsp. *robusta* (Stent & Rattray) Meld.
Aristida stipitata Hack. subsp. *spicata* (De Winter) Meld.
Aristida stipoides Lam.
Tragus berteronianus Schult.
Tragus racemosus (L.) All.
Perotis patens Gand.
Sporobolus sp. R. Br.
Sporobolus coromendalianus (Retz.) Kunth
Sporobolus fimbriatus (Trin.) Nees
Sporobolus ioclados (Trin.) Nees
Sporobolus panicoides A.Rich.
Sporobolus spicatus (Vahl) Kunth
Sporobolus tenellus (Sprengel) Kunth
Sporobolus welwitschii Rendle
Eragrostis sp. Beauv.
Eragrostis aspera (Jacq.) Nees
Eragrostis cilianensis (All.) F.T. Hubb.
Eragrostis dinteri Stapf
Eragrostis echinochloidea Stapf
Eragrostis jeffreysii Hack.
Eragrostis lappula Nees
Eragrostis lehmannniana Nees
Eragrostis nindensis Fical. & Hiern
Eragrostis pallens Hack.
Eragrostis pilosa (L.) Beauv.
Eragrostis porosa Nees
Eragrostis rigidior Pilg.
Eragrostis rotifer Rendle
Eragrostis superba Peyr.
Eragrostis trichophora Coss. & Dur
Eragrostis viscosa (Retz.) Trin.
Microchloa caffra Nees
Cynodon dactylon (L.) Pers.
Enteropogon macrostachys (A. Rich.) Benth.
Chloris gayana Kunth
Chloris virgata Swartz
Acrachne racemosa (Roem. & Schult.) Ohwi
Dactyloctenium aegyptium (L.) Willd.
Dactyloctenium giganteum Fischer & Schweick.

Pogonarthria fleckii (Hack.) Hack.
Pogonarthria squarrosa (Licht. ex Roem. & Schult.) Pilg.
Diplachne fusca (L.) Beauv.
Odyssea paucinervis (Nees) Stapf
Triraphis schinzii Hack.
Enneapogon cenchroides (Roem. & Schult.) C.E. Hubb.
Enneapogon desvauxii Beauv.
Enneapogon scoparius Stapf
Schmidtia pappophoroides Steud.
Elytrophorus globularis Hack.

Family: **CYPERACEAE**
Cyperus amabilis Vahl
Cyperus compressus L.
Cyperus esculentus L.
Cyperus fulgens C.B. Cl.
Cyperus longus L.
Cyperus margaritaceus Vahl
Cyperus sphaerospermus Schrad.
Mariscus chersinus N.E. Br.
Mariscus confusus Vorster
Kyllinga alba Nees
Fuirena sp. Rottb.
Schoenoplectus corymbosus (Roth. ex Roem. & Schult.) J.Raynal
Schoenoplectus erectus (Poir.) Palla ex J. Raynal
Schoenoplectus muricinux (C.B. Cl.) J. Raynal
Schoenoplectus praelongatus (Poir.) J. Raynal
Eleocharis limosa (Schrad.) Schult.
Fimbristylis hispidula (Vahl) Kunth

Family: **COMMELINACEAE**
Commelina africana var *krebsiana* (Kunth) C.B. Cl.
Commelina forskalaei Vahl
Commelina livingstonii C.B. Cl.
Commelina subulata Roth.

Family: **LILIACEAE**
Gloriosa subperba L.
Ornithoglossum vulgare B. Nord.
Trachyandra laxa (N.E. Br.) Oberm.
Trachyandra arvensis (Schinz) Oberm.
Eriospermum abyssinicum Bak.
Eriospermum bakeranum Schinz
Eriospermum omahekense Engl. & Krause
Aloe esculenta Leach
Aloe zebrina Bak.
Albuca sp. L.
Albuca amboensis (Schinz) Oberm.
Urginia sp. Steinh.
Dipcadi sp. Medik.
Dipcadi bakeranum Bolus
Dipcadi longifolium (Lindley) Bak.
Ornithogalum seineri (Engl. & Krause) Oberm.
Ornithogalum stapfii Schinz
Ledebouria undulata (Jacq.) Jessop
Sansevieria pearsonii N.E. Br.
Protasparagus sp. Oberm.

Family: **AMARYLLIDACEAE**
Nerine laticoma (Ker-Gawl.) Dur. & Schinz
Ammocharis coranica (Ker-Gawl.) Herb.
Ammocharis tinneana (Kotschy & Peyr.) Milne-Redh. & Schweick.
Pancratium tenuifolium Hochst. ex A. Rich.

Family: **IRIDACEAE**
Lapeirousia vaupeliana Dinter

Lapeirousia bainesii Bak.

Family: **ORCHIDACEAE**
Eulophia speciosa (R. Br. ex Lindl.) H. Bol.
Eulophia hereroensis Schlechter

DICOTYLEDONAE

Family: **MORACEAE**
Ficus cordata Thunb.

Family: **LORANTHACEAE**
Tapinanthus oleifolius (Wendl.) Danser

Family: **OLACACEAE**
Ximenia americana L. var *microphhylla* Welw. ex Oliv.
Ximenia caffra Sond. var. *caffra*

Family: **POLYGONACEAE**
Polygonum hystriculum Schuster
Polygonum limbatum Meisn.
Oxygonum alatum Burch.

Family: **CHENOPODIACEAE**
Lophiocarpus tenuissimus Hook. fil.

Family: **AMARANTHACEAE**
Hermbstaedtia linearis Schinz
Hermbstaedtia odorata (Burch.) T. Cooke
Sericorema sericea (Schinz) Lopr.
Kyphocarpa angustifolia (Moq.) Lopr.
Cyathula hereroensis Schinz
Leucosphaera bainesii (Hook. fil.) Gilg
Pupalia lappacea (L.) Juss.
Achyranthes sicula (L.) All.

Family: **NYCTAGINACEAE**
Boerhavia diffusa L.

Family: **AIZOACEAE**
Limeum argute-carinatum Wawra & Peyr.
Limeum fenestratum (Fenzl) Heimerl
Limeum myosotis H. Walter
Limeum sulcatum (Klotzsch) Hutch.
Gisekia africana (Lour.) O. Kuntze
Mullugo nudicaulis Lam.
Hypertelis sp. E. Mey. ex Fenzl
Sesuvium sesuvioides (Fenzl) Verdc.
Trianthema triquetra Willd. subsp. *triquetra*

Family: **PORTULACACEAE**
Talinum arnotii Hook. fil.
Talinum tenuissimum Dinter
Portulaca hereroensis Schinz
Portulaca kermesina N.E. Br.
Portulaca quadrifida L.

Family: **CARYOPHYLLACEAE**
Polycarpaea corymbosa (L.) Lam.
Polycarpaea eriantha Hochst. ex A. Rich.

Family: **NYMPHAEACEAE**
Nymphaea caerulea Savigny
Nymphaea capensis Thunb.

Family: **RANUNCULACEAE**

Clematopsis scabiosifolia (DC.) Hutch.

Family: **BRASSICACEAE**
Coronopus integrifolius (DC.) Sprengel

Family: **CAPPARACEAE**
Cleome angustifolia Forssk. subsp. *diandra* (Burch.) Kers.
Cleome rubella Burch.
Boscia albitrunca (Burch.) Gilg & Benedict

Family: **VAHLIACEAE**
Vahlia capensis (L. fil) Thunb.

Family; **CHRYSOBALANACEAE**
Parinari capensis Harv. subsp. *capensis*

Family: **FABACEAE**
Albizia anthelmintica (A. Rich.) Brongn.
Albizia harveyi Fourn.
Acacia ataxacantha DC.
Acacia erioloba E. Mey.
Acacia erubescens Welw. ex Oliv.
Acacia fleckii Schinz.
Acacia hebeclada DC. subsp. *tristis* A. Schreib.
Acacia kirkii Oliv.
Acacia luederitzii Engl. var. *luederitzii*
Acacia mellifera (Vahl) Benth. subsp. *detinens* (Burch.) Brenan
Acacia reficiens Wawra
Acacia tortilis (Forssk.) Hayne
Dichrostachys cinerea (L.) Wight & Arn.
Elephantorhiza elephantina (Burch.) Skeels
Burkea africana Hook.
Giubortia coleosperma (Benth.) J. Leonard
Baikiaea plurijuga Harms
Bauhinia petersiana Bolle subsp. *macrantha* (Oliv.) Brummitt & J.H. Ross
Tylosema esculentum (Burch.) Schreiber
Cassia absus L.
Cassia biensis (Steyaert) Mendonca & Torre
Cassia italica (Mill.) Lam. ex F.W. Andr.
Hoffmanseggia burchellii (DC.) Benth. ex Oliv.
Peltophorum africanum Sond.
Baphia massaiensis Taub. subsp. *obovata* (Schinz) Brummitt
Crotalaria flavicarinata Bak. fil.
Crotalaria leubnitziana Schinz
Crotalaria platysepala Harv.
Trigonella hamosa L.
Indigofera bainesii Bak.
Indigofera charlieriana Schinz
Indigofera daleoides Benth. ex Harv.
Indigofera fleckii Bak. fil.
Ptycholobium biflorum (E. Mey.) Brummitt subsp. *angolensis* (Bak.) Brummitt
Tephrosia dregeana E. Mey.
Tephrosia lupinifolia DC.
Tephrosia oxygona Welw. ex Bak.
Mundulea sericea (Willd.) A. Chev.
Sesbania macowaniana Schinz
Requiena pseudosphaerosperma (Schinz) Brummitt
Aeschynomene indica L.
Pterocarpus angolensis DC.
Lonchocarpus nelsii (Schinz) Heering & Grimme
Neorautanenia amboensis Schinz
Vigna decipiens Harv.
Otoptera burchellii DC.

Family: **ZYGOPHYLLACEAE**
Tribulus terrestris L.

Tribulus zeyheri Sond.

Family: **BURSERACEAE**
Commiphora africana (A. Rich.) Engl.
Commiphora angolensis Engl.
Commiphora glandulosa Schinz
Commiphora pyracanthoides Engl.
Commiphora tenuipetiolata Engl.

Family: **MALPHIGIACEAE**
Sphedamnocarpus pruriens (Juss.) Szyszyl.

Family: **POLYGALACEAE**
Polygala albida Schinz
Polygala leptophylla Burch.
Polygala pygmaea Guerke
Polygala schinziana Chod.
Securidaca longepedunculata Fresen.

Family: **DICHAPETALACEAE**
Dichapetalum cymosum (Hook.) Engl.

Family: **EUPHORBIACEAE**
Phyllanthus maderaspatensis L.
Phyllanthus omahekensis Dinter & Pax
Phyllanthus pentandrus Schumach. & Thonn.
Croton gratissimus Burch.
Croton menyhartii Pax
Acalypha indica L.
Acalypha segetalis Muell. Arg.
Pterococcus africanus (Sond.) Pax ex K. Hoffm.
Jatropha erythropoda Pax & K. Hoffm.
Cephalocroton mollis Klotzsch
Ricinodendron rautanenii Schinz
Spirostachys africana Sond.
Euphorbia monteiroi Hook. fil.
Chamaesyce inequilatera (Sond.) Sojak

Family: **ANACARDIACEAE**
Sclerocarya birrea (A. Rich.) Hochst.
Ozoroa longipes (Engl. & Gilg.) R. & A. Fernandes
Ozoroa paniculosa (Sond.) R. & A. Fernandes
Rhus marlothii Engl.
Rhus tenuinervis Engl.

Family: **CELASTRACEAE**
Maytenus senegalensis (Lam.) Exell.
Cassine transvaalensis (Burtt Davy) Codd
Salacia sp. L.

Family: **RHAMNACEAE**
Ziziphus mucronata Willd.
Helinus integrifolius (Lam.) O. Kuntze
Helinus spartioides (Engl.) Schinz & Engl.

Family: **TILIACEAE**
Corchorus asplenifolius Burch.
Grewia bicolor Juss.
Grewia flava DC.
Grewia flavescens Juss. var. *flavescens*
Grewia retinervis Burrett
Grewia tenax (Forssk.) Fiori
Grewia villosa Willd.

Family: **MALVACEAE**
Sida ovata Forssk.
Pavonia claturata Mast.

Hibiscus calyphyllus Cav.
Hibiscus micranthus L. fil.
Cienfugosia digitata Cav.
Gossypium triphyllum (Harv.) Hochr.

Family: **BOMBACEAE**
Adansonia digitata L.

Family: **STERCULIACEAE**
Melhania forbesii Planch. ex Mast.
Melhania virescens (K. Schum.) K. Schum.
Hermannia eenii Bak. fil.
Hermannia modesta (Ehrenb.) Mast.
Hermannia tomentosa (Turcz.) Schinz ex Engl.
Waltheria indica L.

Family: **OCHNACEAE**
Ochna cinnabarina Engl. & Gilg
Ochna pulchra Hook.

Family: **ELATINACEAE**
Bergia pentherana Keissl.

Family: **LYTHRACEAE**
Ammannia baccifera L.
Nesaea rigidula (Sond.) Koehne

Family: **COMBRETACEAE**
Combretum apiculatum Sond. subsp. *leutweinii* (Schinz) Exell
Combretum celastroides Welw. ex Laws subsp. *celastroides*
Combretum collinum Fresen subsp. *gazense* (Swynn. & Bak. fil) Okafor
Combretum engleri Schinz
Combretum hereroense Schinz
Combretum imberbe Wawra
Combretum psidioides Welw. subsp. *dinteri* (Schinz) Engl.
Combretum zeyheri Sond.
Terminalia prunioides Laws.
Terminalia sericea Burch. ex DC.

Family: **TRAPACEAE**
Trapa natans L.

Family: **EBENACEAE**
Diospyros lycioides Desf.

Family: **LOGANACEAE**
Strychnos cocculoides Bak.
Strychnos pungens Soler.
Strychnos spinosa Lam.

Family: **GENTIANACEAE**
Sebaea grandis (E. Mey.) Steud.
Enicostema hyssopifolium (Willd.) Verdoorn
Nymphoides indica (L.) O. Kuntze

Family: **APOCYNACEAE**
Diplorhynchus condylocarpon (Muell. Arg.) M. Pichon
Baissea wulfhorstii Schinz

Family: **PERIPLOCACEAE**
Raphionacme sp. Harv.
Raphionacme lanceolata Schinz

Family: **ASCLEPIADACEAE**
Sarcostemma viminale (L.) R. Br.
Brachystelma sp. R. Br.
Ceropegia lugardae N.E. Br.

Ceropegia nilotica Kotschy
Ceropegia pygmaea Schinz
Duvalia polita N.E. Br.
Carulluma lugardii N.E. Br.
Orbeopsis lutea (N.E. Br) Leach
Huernia verekeri Stent
Pergularia daemia (Forssk.) Chior.
Fockea angustifolia K. Schum.
Fockea edulis (Thunb.) K. Schum.

Family: **CONVOLVULACEAE**
Evolvulus alsinoides (L.) L.
Seddera suffruticosa (Schinz) Hall fil.
Convolvulus sagittatus Thunb.
Merremia palmata Hall fil.
Merremia tridentata (L.) Hallier fil. subsp. *angustifolia* (Jacq.) Ooststr.
Merremia verecunda Rendle
Ipomoea adenioides Schinz
Ipomoea bolusiana Schinz
Ipomoea coptica (L.) Roth. ex Roem. & Schult.
Ipomoea magnusiana Schinz
Ipomoea obscura (L.) Ker-Gawl.
Ipomoea sinensis (Desr.) Choisy subsp. *blepharosepala* (Hochst. ex A. Rich.) Verdc.
Ipomoea verbascoidea Choisy

Family: **BORAGINACEAE**
Ehretia rigida (Thunb.) Druce
Heliotropium nelsonii C.H. Wright
Heliotropium ovalifolium Forssk.
Heliotropium strigosum Willd.
Trichodesma angustifolia Harv.

Family: **VERBENACEAE**
Lantana angolensis Mold.
Plexipus pinnatifidus (L. fil) Fernandes
Clerodendrum ternatum Schinz
Clerodendrum uncinatum Schinz

Family: **LAMIACEAE**
Tinnea rhodesiana S. Moore
Acrotome inflata Benth.
Plectranthus tetensis (Bak.) Agnew
Hemizygia bracteosa (Benth.) Briq.
Becium obovatum (E. Mey.) N.E. Br.

Family: **SOLANACEAE**
Solanum delagoense Dunal.
Solanum kwebense N.E. Br.
Solanum multiglandulosum Bitter

Family: **SCROPHULARIACEAE**
Aptosimum decumbens Schinz
Limnophila sp. R. Br.
Craterostigma plantagineum Hochst.
Alectra parvifolia Schinz
Striga asiatica (L.) Kuntze
Striga elegans Benth.
Striga gesneriodes (Willd.) Valke ex Engl.

Family: **BIGNONIACEAE**
Rhigozum brevispinosum O. Kuntze
Catophractes alexandri D. Don.

Family: **PEDALIACEAE**
Pterodiscus luridus Hook. fil.
Harpagophytum procumbens DC. ex Meissn.

Sesamum triphyllum Welw. ex Aschers.
Dicerocaryum eriocarpum (Decne) Abels

Family: **LENTIBULARIACEAE**
Utricularia sp. L.

Family: **ACANTHACEAE**
Petalidium engleranum (Schinz) C.B. Cl.
Petalidium variabile (Engl.) C.B. Cl.
Ruelliopsis damarensis S. Moore
Ruellia patula Jacq.
Barleria lancifolia T. Anderson
Barleria senensis Klotzsch
Blepharis diversispina (Nees) C.B. Cl.
Blepharis mitrata C.B. Cl.
Hygrophila pilosa Burkill
Monechma divaricatum (Nees) C.B. Cl.

Family: **RUBIACEAE**
Kohautia sp. Cham. & Schlechtd.
Ancyclanthos bainesii Hiern

Family: **CUCURBITACEAE**
Corallocarpus bainesii (Hook. fil.) A.Meeuse
Acanthosicyos naudinianus (Sond.) C. Jeffrey
Momordica balsamina L.
Citrillus lanatus (Thunb.) Matsumura & Nakai
Cucumis sp. L.
Coccinia rehmannii Cogn.
Coccinia sessilifolia (Sonder) Cogn.

Family: **LOBELIACEAE**
Lobelia depressa L. fil.

Family: **ASTERACEAE**
Erlangea schinzii O. Hoffm.
Vernonia fastigiata Oliv. & Hiern
Felicia clavipilosa Gran.
Felicia anthemidodes (Hiern) Mendonca
Nidorella resedifolia DC.
Tarchonanthus camhoratus L.
Geigeria otaviensis (Merxm.) Merxm.
Geigeria schinzii O. Hoffm.
Xanthium strumarium L.
Melanthera marlothiana O. Hoffm.
Bidens biternata (Lour.) Merr. & Sherff.
Eriocephalus pubescens D.C.
Rennera limnophila Merxm.
Senecio schinzii O. Hoffm.
Senecia longiflorus (DC.) Sch. Bip.
Hirpicium gazanioides (Harv.) Roessl.
Hirpicium gorterioides (Oliv. & Hiern) Roessl. subsp. *gorterioides*