

7 A PLANT ECOLOGICAL SURVEY OF THE
UMFOLOZI GAME RESERVE
ZULULAND

by

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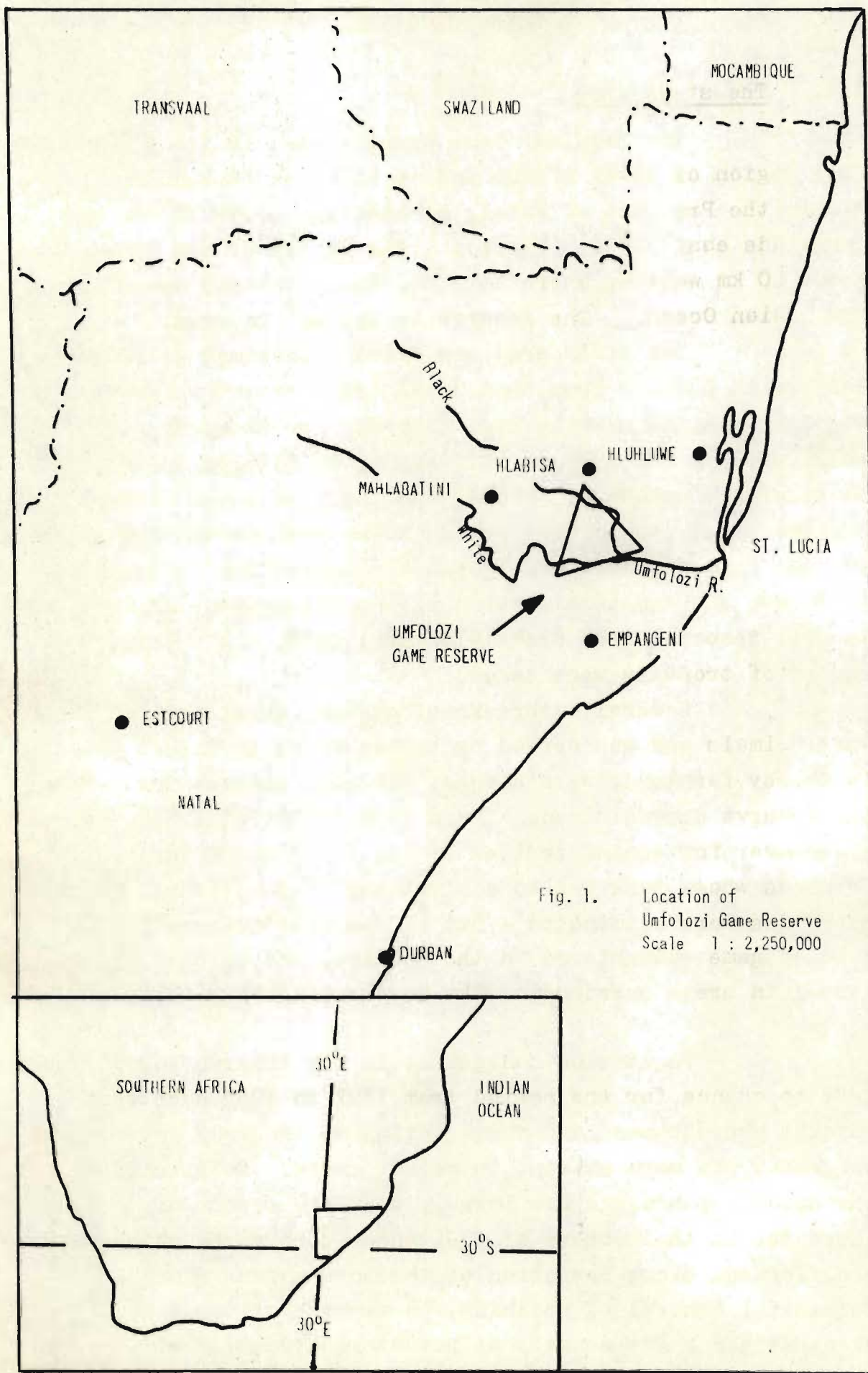
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CHAPTER ONE

INTRODUCTION

1.1. The study area

The Umfolozi Game Reserve lies in the summer rainfall region of South Africa and is situated in Zululand, within the Province of Natal, at latitude south $28^{\circ}20'$ and longitude east $31^{\circ}50'$ (Fig.1). The centre of the Reserve is about 50 km west of where Lake St. Lucia Estuary opens into the Indian Ocean. The Reserve is 493 km^2 in area.

The study area was first proclaimed as a Game Reserve in 1897. From then until 1947 the entire Reserve was deproclaimed over several periods, for the years 1920, 1932 to 1939, and 1945 to 1947 (Vincent, 1970, pp 13-16). A considerable amount of illegal hunting took place in the Reserve since its initial proclamation even though the shooting of game in some parts was supposedly controlled by issue of licences; the southern portion of the Reserve was defined as a Special Shooting Area from 1916 until 1918, and a large number of trophies were taken.

Several outbreaks of nagana, which originated in game animals and was spread by tsetse flies to infect cattle in nearby farmland, were amongst the main reasons for having the Reserve deproclaimed. From 1932 to 1951 the Reserve was given over for administration by the Division of Veterinary Services whose task was to control the tsetse flies. By 1952 the flies were eliminated - but at the cost of some 30,000 head of game slaughtered in the Reserve, and an even larger number in areas surrounding the Reserve (Mentis, 1970, pp 366 - 373).

Vegetation management in the Reserve was virtually left to chance for the period from 1897 to 1952 such that thicket encroachment and over-grazing of the veld have become progressively more evident in recent years. Deterioration of the natural pasturage has largely been the result of marked increases in the numbers of indigenous herbivores which have proliferated since cessation of the anti-nagana slaughter. Successful control of poaching, an absence of epidemic diseases and a low density of predators have allowed the

herbivore proliferation. Over-grazing might have been aggravated through the necessary construction of fences along the east, south and west boundaries of the Reserve. Animal migrations, which might otherwise have taken place during times of drought or over-population, have been discouraged by the fence, by farming and by other human disturbance beyond the fence, so that the herbivores are largely confined within the sanctuary of the Reserve.

Effective conservation of the vegetation and animals has been made possible since 1952 when the Reserve was placed under the direct control of the Natal Parks, Game and Fish Preservation Board. The Natal Parks Board aims at producing a scientifically based plan for the management of the Reserve and, towards this end, requested the author, in 1967, to study the ecology of plant communities in the Reserve. The results of the study are embodied in this thesis.

1.2. Objectives and presentation

The main objectives of the study were to identify, describe and map the plant communities of the Reserve and to explain, as far as possible, some features of their succession and ecological relationships. The capability of the veld to support the associated animals was also to be investigated.

Some physical background needed for an understanding of the vegetation is given in Chapter Two by an account of the topography, geology, soils and climate. A topography map provided consists of the South Africa 1:50,000 sheets issued by the Government Printer, Pretoria; the sheet references being 2831: BA, BB, BC, BD. The topography map includes place names, most of which are written in Zulu. The Zulu spellings are controversial and those written on the topography map often differ from those in the text. The text spellings were supplied by Mr John Vincent on the authority of Mr R. Mayne, Zulu linguist and law court interpreter, and are regarded as being the more accurate. A place names map giving accurate spellings is, therefore, provided in addition to the topography map. Copies provided of topography, landsurface, geology and vegetation maps are all drawn to a scale of 1:50,000 so that a direct comparison

is possible. All the maps are placed in Appendix I which is a folder located on the front cover of this book.

INSERT APPENDIX I ON FRONT COVER

Chapter Three is devoted to methods used for investigation of the vegetation. The main part of this study is presented in Chapter Four which is an account of the plant ecology. The various plant communities are physiognomically described with the aid of photographs, and are floristically described through reference to tables giving quantitative floristic composition. The extent and distribution of the communities is portrayed in the vegetation map given in Appendix I. Plant names are given to specific level in the text, but are fully quoted with authorship included in Appendix II, which is a check list of all plants recorded in the Reserve.

INSERT APPENDICES II and III NEAR BACK COVER

Some biotic influences are mentioned in Chapter Five which also contains a brief historical record of human and animal populations. A list of the larger mammals in the Reserve is given in Appendix III. Chapter Six contains an evaluation of the procedures used for investigation of the vegetation as well as a general discussion on the plant ecology. This leads to some management recommendations offered in Chapter Seven which may mainly be of interest to personnel of the Natal Parks Board.

All photos in this report were taken by the author except for Photo 16 which was kindly lent by Mr D. Rowe-Rowe. A white rod shown in some of the photos is a marker one metre in length. The localities where the photos were taken are indicated on the landsurface map; the numbers on the map coincide with the photo numbers given in the text, and the arrows give the camera direction.

A summary and a list of cited references are provided near the end of this report. The recommendations of the Committee on Form and Style of the Conference of Biological Editors (Anon., 1964) were generally followed for

the usage of abbreviations, of decimal points and of commas in numerals.

This report can be regarded as an inventory and partial explanation of some features in the Reserve; and should be of some use as a background for management, as a source of ancillary information for other research, and as a guide for the preparation of displays which could help visitors to understand and enjoy the wilderness of the Reserve.

1.3. Acknowledgements

The assistance given by many people during the course of this study is gratefully acknowledged.

I am particularly indebted to my supervisors in the University of Natal. The most helpful tutelage and considerable time afforded me by Professor Emeritus A.W.Bayer, F.R.S.S.Afr., is truly appreciated. Professor C. H. Bornman kindly made available the facilities of the Botany Department and commented on the text. The advice of Professor J. O. Grunow, now at the University of Pretoria, improved the presentation of quantitative plant data.

Other members of the University staff freely gave assistance. Dr Kathleen Gordon-Gray and Dr Olive Hilliard identified herbarium specimens. Professor J.F.V. Phillips commented on vegetation physiognomy. Professor Lester King dated the main geomorphological events and checked the section on geology. Professor D. Scogings advised on photogrammetry and map compilation. Mr R. Schulze provided some insolation data and arranged for the loan of equipment from the Geography Department. Mr D. Webb authorised use of facilities in the University Computer Centre.

Assistance was received from some Government Departments. In particular, Dr D. Edwards of the Botanical Research Institute is thanked for lessons in photo interpretation; useful discussions were held with him and his staff, notably Mr J. Morris who was consulted on some statistical and computational matters. Mr R. Ludorf at the Cedara College of Agriculture kindly identified soils and arranged for the chemical analysis of grass samples. Mr R. T. Rudd of the Department of Water Affairs supplied evaporation data from

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This study was made possible through the foresight and generosity of my employer, the Natal Parks, Game and Fish Preservation Board. My superiors, notably Professor R. C. Bigalke (now at the University of Stellenbosch), Mr R. S. Crass and Dr D. R. M. Stewart, have given encouragement at all times. Mr John Vincent arranged field facilities, and the cooperation of Mr Ian Player and his Zululand staff is appreciated. Mr M. Nkosi was a helpful field assistant. Some stimulating discussions were held with my colleagues, Mr O. Bourquin (plant identification), Mr M. Mentis (herbivore biomass), and Mr N. Owen-Smith (white rhinoceros behaviour).

Mrs. Margaret Hofmeyr ably drafted the diagrams, helped in compiling the maps and produced the working copies. Miss Heather Francis kindly prepared the final map copies. I am particularly indebted to Mrs Thelma Anderson for her competent typing of past and present copies of this report. Miss Dorianne Morton kindly assisted with typing the tables.

* * * * *

CHAPTER TWO

PHYSICAL FACTORS

2.1. Topography

Most of the topographic features of the Reserve described below are shown on the topography map. Place names, spelt correctly, can also be located on the place names map.

INSERT TOPOGRAPHY AND PLACE NAMES MAPS AT APPENDIX I

The area of the Reserve is part of two great valleys carved out by the Black and White Umfolozi Rivers which flow near the northern and southern boundaries respectively. The Rivers enter the Reserve from the west; their sluggish and meandering courses (Photo 1) gradually converging towards and finally meeting at their confluence in the east.

INSERT PHOTO 1

An almost wedge shaped watershed of higher lying ground, broadest in the west at about 20 km wide and diminishing to a point at the confluence in the east, protrudes across the centre of the Reserve and separates the rivers. Starting from the highest point, Zintunzini at 579m altitude on the western boundary of the Reserve, the watershed falls irregularly in altitude through a series of ridges until it meets the confluence, the lowest point in the Reserve at an altitude of about 45m, on the east boundary.

The summit of Khukho in the north-west is a good vantage point for obtaining a general view of the Reserve and its surroundings. Westwards, scarred and heavily over-grazed farm country beyond the Reserve's boundary rises steadily towards Mahlabatini (Fig.1) at 843m altitude. Northwards, the observer peers down into the great trough of the Black Umfolozi Valley. Beyond the Valley a clear view is obtained of the blue-green Hlabisa Heights, altitude 512m, which stand out as a ridge along the horizon well beyond the Reserve's



Photo 1. The Black Umfolozi River (middle distance) flows sluggishly, from left to right, along its gently graded, sinuous channel on the low lying, rather flat, Quaternary Surface. Various woodland communities stretch for several kilometres in all directions from the River. In the foreground, succulent Aloe marlothii is protected by some dead, persistent leaves from fires which occasionally burn the Themeda Grassland. Mpila, 9.5.70.



Photo 2. Sediments of the Beaufort Series constitute a parallel series of small ridges and valleys in the east of the Reserve as far as the White Umfolozi River, which flows from left to right across the centre of the photo. An Open Woodland of Acacia tortilis occupies the ridge tops, and a denser, Closed Woodland of Spirostachys africana occupies stream banks. Mqizweni Pan lies in a depression close to the near bank of the River, right of centre. From the far bank, various woodland communities, fully exposed to the sun, stretch interminably to beyond the horizon. Ciyana, 7.7.70.

northern boundary. Small patches of green forest, not represented anywhere in the drier Reserve, are just discernible along small valleys on the south aspect of the Hlabisa Heights. Looking to the east, which takes into view most of the Reserve, and to the south, a scenery of interminable small ridges, hills and valleys, stretches ever onwards across the hazy, blue-grey vista to merge with the Zululand Coast Plain on the far horizon. The low-lying course of the White Umfolozi River to the south lies concealed from view behind the hills.

The repetitive monotony of the hills and valleys is repeated by their rather featureless and seemingly uniform vegetative mantle which, at a distance, appears as a tree studded grassveld. Closer examination shows, however, that the trees are sparsely distributed on the hill tops, are denser on the hill slopes, and are densest along the valley bottoms. This pattern is endlessly repeated, with but few minor variations, from hill to hill and from valley to valley (Photo 2).

INSERT PHOTO 2

More attractive views of the Reserve are seen on clear days at dawn and in the late afternoon when an interplay of sunlight and shadow emphasises relief. The early rays of sunshine pick out a cool, amber toned mosaic of the east and north-east aspects of the many hills and hillocks which contrasts against dappled shadows representing south and west aspects. The pattern is progressively lost as the sun climbs higher and, by mid-morning, most of the Reserve apart from a few, steep south aspect scarps is bathed in sunshine. But as the sun declines in the late afternoon, a new mosaic gradually emerges when west and south-west aspects show up in warm browns, whilst north-east aspects submerge into shadows.

Broad topographic features are most easily described on a basis of three land surfaces, of Miocene, Pliocene and Quaternary ages, which were found to constitute the landscape of the Reserve. Each land surface was found to possess some characteristic and fairly easily recognisable features as described below. The extent and distribution of

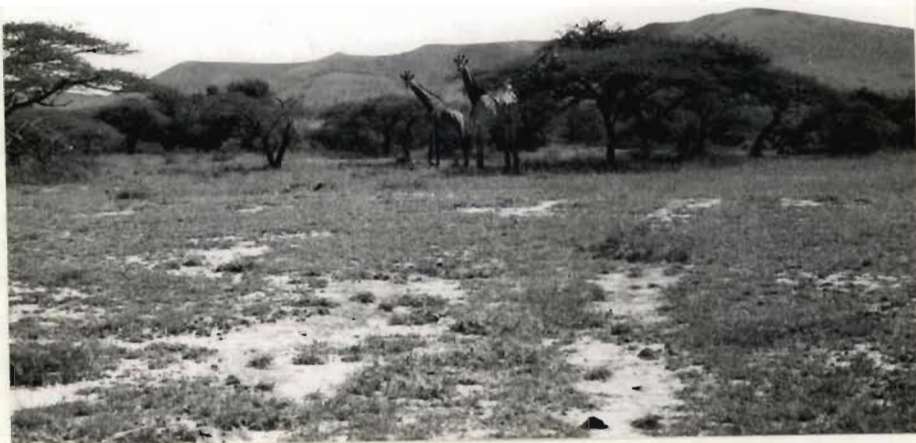


Photo 3. The oldest, Miocene Surface shows on the skyline formed by Zintunzini Hill, which stands about 200m above the younger, Pliocene Surface in the foreground. The debris slopes of Zintunzini, facing the camera, are also of Pliocene age. Giraffe browse off the umbrella shaped crowns of Acacia tortilis. A heavily grazed Panicum coloratum grass Community is too sparse for the passage of fire. Bizo area, 15.3.69.



Photo 4. The skyline and upper portion of this 150m high, partially fragmented, north-west aspect debris-slope are of Pliocene age. The lower portion and the reed colonised bed of the White Umfolozi (foreground) are of youngest, Quaternary age. The River is scarcely flowing during a dry season. A Combretum apiculatum Closed Woodland covers the debris-slope. Ndleke, 6.7.70.

the three land surfaces is shown on the land surface map located in Appendix 1. This map was drawn by taking into account some conspicuous changes in gradient shown by contours on the topography map, and by correlating the gradient changes with certain features including nickpoints, boulder beds, changes in soil colour and depth, seen in the field.

INSERT LANDSURFACE MAP AT APPENDIX 1

INSERT PHOTO 3

The oldest or Miocene Surface of the Reserve is represented only on and near the summits of the higher hills which stand out clearly against the skyline, such as Zintunzini (Photo 3), and which are, therefore, the most useful of landmarks. These hills are, reading from west to east on the topography and place names maps, as follows: Zintunzini at 579m, Ntoiyana at 476m, Khukho at 465m, Sokwezele at 462m, Nqolothi at 429m, Mantiyane at 366m, Mbulungu at 339m, Chibilenyathi at 369m, Mpila at 344m, Luthelezi at 341m, Mduba at 355m, Dengezi at 303m, Matshemnyama at 264m, and finally, at the south-eastern corner of the Reserve, is Ciyana at 246m.

A pattern of diminishing altitudes from west to east shown by the Miocene hills above is evidence that the Reserve and its surrounding country are situated on the eastern flank of the Natal Monocline that dips east by about one degree towards the Indian Ocean. The topographic features of the Reserve have largely resulted from a number of upheavals, each followed by an erosional cycle, on the Monoclinial flank (Professor L. King, pers. com.)

Towards the end of Miocene times an upheaval elevated the Miocene Surface in the west of the Reserve by an estimated 240m or so, and by a lesser amount in the east. The 240m elevation is estimated by subtracting the lower altitudinal limit of the Pliocene Surface from that of the Miocene Surface. Elevation in the east was lower because, according to Professor King (pers. com.), uplift was greater towards the interior in the west than nearer the coast in the east.



Photo 5. A broad tract of gently undulating country (centre), is part of the Pliocene Surface sculptured by pedimentation. Lubisana Hill which rises to the skyline on the left is a Miocene remnant, as is Mantiyane on the right (middle distance), spared from Pliocene pedimentation. A crown of Combretum apiculatum is in the lower righthand corner. Mphafa catchment seen from Mpila encane, 8.5.70.



Photo 6. A forty metre high scarp incised through the horizontally stratified, Table Mountain Series by the White Umfolozi during Quaternary times is on the left bank. A white, sandy, slip-off slope is on the right bank. Mhlolokazana, 4.7.70.

During an ensuing quiescent period the newer Pliocene Surface of the Reserve was formed where river incision and pedimentation stripped away nearly all of the older Miocene Surface. Evidence of incision by the White Umfolozi River is seen at the upper parts of the rugged, near vertical scarps formed on more resistant rocks, dolerite and sandstone, at Mpila, Momfu and Ndleke (Photo 4). Extensive pedimentation produced large tracts of gently undulating country which are a main feature of the Pliocene Surface. One of these tracts, stretching at least 14 km from between Mbulunga in the north to Iubisana in the south, contains considerable portions of the catchments of the Thobothi, Khandeledube, Gqoyini, Mphafa (Photo 5) and Madlozi Streams. Many steep debris slopes and hill slopes that sweep upwards to the Miocene Surface, such as the near 45 degree hill slopes on the eastern aspect of Zintunzini (Photo 3), are also part of the Pliocene Surface which resulted from pedimentation.

INSERT PHOTOS 4, 5

A second upheaval late in Cainozoic times uplifted the Miocene and Pliocene Surfaces by about 40m in the west and by a lesser amount in the east - as shown by altitudinal differences between the Pliocene and Quaternary Surfaces.

During the ensuing, quiescent Quaternary period the most recent Quaternary Surface was formed where much of the earlier Pliocene Surface was eroded away, mostly through river action. The Black and White Umfolozi Rivers were rejuvenated; their beds were deeply incised such that the scarp at Mpila now totals 150m high, the scarp at Momfu 60m, and the Ndleke scarp 150m. In addition, a new, 40m high scarp entirely of Quaternary age was formed by the White Umfolozi at Mhlolokazana (Photo 6). The greater extent of the Quaternary Surface consists, however, of broad, fairly level valley plain terraces (King, 1951, p 175) also known as alluvial terraces. Some magnificent views of these terraces are possible from hill summits on the Miocene Surface, as at Mpila, and from the edge of the scarps, as at Momfu (Photo 7). The almost flat alluvial terraces can be seen to extend as



Photo 7. Waters of the White Umfolozi River have receded to a sluggish flow and have revealed a wide sandy bed as the dry season sets in. A fairly level alluvial terrace, typical of the Quaternary Surface, stretches outwards from the River towards hills of the Miocene Surface on the left horizon, and towards island-like Ngabaneni Hill, which is a Pliocene remnant, on the right horizon. The darker trees on the right bank of the River are of Riverine Woodland. Succulent Euphorbia tirucalli grows on rocks near the lower right corner. South west view from Momfu, 8.5.70.



Photo 8. The V cross-section of a typical, rocky drainage line. The many rocks protect saplings from fire so that a Closed Woodland of Spirostachys africana and Euphorbia tirucalli grows in the background. A smooth-barked, lightly toned tree of Commiphora neglecta (left, middle distance) has shed its leaves, as has a spinescent shrub of Dichrostachys cinerea growing in the centre of the drainage line. Mbuzane area, 9.5.70.

far as four kilometres outwards from both banks of the Black and White Umfolozi Rivers. Less extensive alluvial terraces are also seen on the Quaternary Surface in places along the lower reaches of all tributary streams, but are more conspicuous along the Gqoyini and Mphafa Streams.

INSERT PHOTOS 6, 7

Drainage of the Reserve is effected through many unnamed drainage lines, several streams, and the Black and White Umfolozi Rivers.

The drainage lines and streams are responsible for minor topographic features of smaller valleys, hillocks and gentle rises which break up and add variety to the major features of the Reserve, whether the tops of the high hills comprising the Miocene Surface, or the steep debris slopes and gently undulating country characteristic of the Pliocene Surface, or the broad, rather flat alluvial terraces extensive on the low-lying, Quaternary Surface.

The drainage lines are mostly found on the higher country near hill tops and on steeper hill slopes. The drainage lines usually have, therefore, rather steep gradients, anywhere from about 50 to 10 degrees, and rocky, V-section channels (Photo 8). A drainage line runs in an almost straight course down slope for a short distance of not usually more than one kilometre before more gentle terrain is encountered, and where it will open into a stream.

INSERT PHOTO 8

All streams in the Reserve are tributaries of either the Black or the White Umfolozi Rivers. The larger streams in the Reserve (reading clockwise from the north-west corner of the place names map) include the Thobothi, Gqoyini, Thumbu, Ketheni, Fuyeni, Gome, Munywane, and the Madlozi in the south-west. The Mphafa and Mfulamkhulu drain from the west-central part of the Reserve into the White Umfolozi. The streams mostly lie in slightly sinuous courses having gentle gradients of about five degrees and less. The streams, when viewed in cross section, typically show



Photo 9. The vertical, earthen bank of the stream has been eroded to reveal plant roots, which are confined to the A soil horizon and which do not penetrate the hard B horizon. Finely plated, black, Lower Ecca shale (foreground) occupies the dry stream bed. A white tufa of carbonate salts, about 30cm thick, is deposited on the shale (behind the feet of the figure). Bed of Munywane Stream, 23.7.68.



Photo 10. The Gqoyini is a typical stream which, in common with all other streams and drainage lines in the Reserve, flows only during rainy spells. Note the black silt, a result of soil erosion, trapped to capacity on the upstream (right) side of the causeway, and the debris of dead trees deposited by floodwaters on the downstream (left) side. Dark green foliage of a large tree of Schotia brachypetala is seen to the left of the Spirostachys Closed Woodland on the far bank. The foreground includes a leafy seedling of Euclea shimperi and some grasses of Bothriochloa insculpta in flower. Gqoyini Stream, 9.5.70.



Photo 11. The pool of water in the Mphafa Waterhole (foreground) is stored over from an unseasonal rain storm in the dry season. The Waterhole is part of the most recent, Quaternary Surface. The figure stands on the older, Pliocene Surface. A nickpoint, being the almost vertical rock face lying from below the figure's feet to just below the water surface, is the intersection between the two Surfaces. The nickpoint is on horizontally bedded Middle Ecca sandstone, where tall Euphorbia tirucalli and rosette-like Aloe vanbalei grow. Acacia spp. and Spirostachys africana are on the Pliocene Surface behind the figure. Mphafa Waterhole, 6.5.70.



Photo 12. The Fuyeni Stream flows from the left to meet the well grassed, broad slip-off slope on the south bank of the White Umfolozi, which lies to the right but is not included by the photo. Horses (small) and white rhino (large) graze a coarse Grassland on the slip-off slope in the foreground. Dark trees of Acacia robusta and pale reedbeds occupy part of the bed of the Fuyeni Stream. Makamisa, 6.7.70.

almost vertical earth banks, from one to three or more metres deep (Photo 9), and have flat bottoms from two to ten or more metres wide (Photo 10).

INSERT PHOTOS 9, 10

Of particular interest is a distinct break or nickpoint (King, 1951, p 174) seen in the bed of the Mphafa Stream at the Mphafa Waterhole (Photo 11) at the 168m (or 550 ft) contour. The stream bed falls some five metres at the nickpoint so that a waterfall is seen when the stream flows. This nickpoint marks a point where the upper and older Pliocene Surface is intersected by the lower and younger Quaternary Surface. The Mphafa flows through a mature, fairly wide valley with gently sloping flanks on the Pliocene Surface above the nickpoint, and through a youthful narrow valley having steep flanks on the Quaternary Surface below the nickpoint.

INSERT PHOTO 11

The Black and White Umfolozi Rivers flow sluggishly westwards at gentle gradients averaging at about 0.6 metres per kilometre. Their channels vary in width between a minimum of 50m to a maximum of 500m and follow meandering paths which, in many places, as at Mhlolokazana (Photo 6), Ndleke (Photo 4), Mahobobosheni and Makamisa along the White Umfolozi, turn tortuously and suddenly change direction. At these and other places where a river suddenly changes direction, the under-cut slope or bank of the river typically lies immediately against a towering, rugged Quaternary scarp; whilst the slip-off slope on the opposite bank consists of a broad, even up to 500m wide in extreme examples as at Makamisa (Photo 12), expanse of sand that is grassed or bare. However, for the greater part of their courses where the Rivers run more or less straight, they are lined by sand banks about 25m wide and about five metres high. The sand banks most often pass, with a small increase of one or two metres in altitude, into flanking red to orange coloured soils of the Quaternary alluvial terraces.



Photo 13. These small pans were filled by surface runoff following an unseasonal rainstorm during the dry season. Trees of Acacia nilotica (left) and A. tortilis (centre and right) are present. Sparse, heavily grazed and trampled Urochloa mossambicensis grass surrounds the pans which are used by animals for drinking and wallowing. Madlozi, 9.5.70.



Photo 14. A recently formed gulley - note plant roots exposed on the right bank but confined to the more permeable, upper part of the soil profile. Such gullies are found in most bottomlands of the Reserve and result from over-grazing of a once protective grass cover. A few grasses forming the now sparse cover include Panicum maximum (lower corner, left) and Sporobolus nitens (on the brink of the far bank of the gulley and towards the right). Some white carbonate nodules, typical of soils of the Bottomland Association, are exposed in the far bank. Near Gqoyini Stream, 6.5.70.

INSERT PHOTO 12

2.2. Water

Surface water in the Reserve is abundant only during the rainy summer season which extends from October to March inclusive, when 72 percent of the mean annual rainfall is recorded. Water can be found at times, but not always, during this period in many places fairly well distributed over the Reserve, whether in small pans, in drainage lines or streams. But water is scarce during the dry winter season, from April to September inclusive, when 28 percent of the rainfall is recorded. The small pans, drainage lines and streams are then normally bone dry, and water is obtainable only from a few widely separated perennial sources, including a few springs, one or two large pans, and the two Rivers.

2.2.1. Seasonal water

Many small pans, rarely more than ten metres in diameter, scattered about the Reserve are filled only by surface runoff following rainstorms (Photo 13). Their waters persist for but short periods of several weeks and, if not replenished, dry out because of high evaporation. Some of the smaller pans develop where animals, including warthog and rhinoceros, wallow in a depression formed where an antbear has burrowed into a termite mound. The depression is filled by runoff and is gradually enlarged over the years by wallowing animals. An impervious clay seal forms on the floor of the depression so that water does not easily seep out.

INSERT PHOTOS 13, 14

For the greater part of the year, particularly during the dry season, there is no visible water flow in any drainage line or stream in the Reserve. Water rushes in sudden torrents down the drainage lines and streams only during and after rain storms. After rain storms flow persists



Photo 15. The stagnant, perennial water of Mgqizweni Pan is lined in places by reedbeds. The water is replenished by seasonal flow of the Mgqizweni Stream, which enters from the south, and by occasional overflows when floods overtop the banks of the White Umfolozi River. The River lies 200m north of the Pan, but the two are not directly connected by a channel. View from the north shore of Mgqizweni Pan, 4.7.70.



Photo 16. The crest of a small, turbulent flood approaches down the White Umfolozi River and over-rides the slower, calmer waters of normal flow seen on the left. Riverine Woodland grows on deep sand of the far bank. Ngubeni, 7.4.63. Photographed by D. Rove-Rove.

for a few hours in the drainage lines, and for one or two days, depending on the amount and duration of rainfall, in the streams.

Flood waters of all streams in the Reserve are always densely turbid from soil eroded out of the catchments. Photo 10 illustrates some of the silt load of the Gqoyini Stream deposited behind a causeway. Extensive gulley systems are developing near all streams because overgrazing has much reduced the protective grass cover (Photo 14).

2.2.2. Perennial water

A few perennial springs present include one in each of the Ntshiyana and Nyonikazana Streams, the Ngomane spring at a source of the Gome Stream, and a spring on Nqolothi Hill. The springs give out little more than an ooze or feeble trickle of rather saline water.

Substantial waters covering a hectare or two are contained throughout most years by the Mgqizweni (Photo 15) and Dadethu Pans. The two pans lie close to the White Umfolozi River; their waters are supplied by overflows from the River, and by seasonal stream flow. The Mgqizweni Pan is known to have dried up twice in recent years, in 1936 and in 1952, whilst the Dadethu has dried up more often (Vincent, 1970, p 9).

INSERT PHOTOS 15, 16

The White Umfolozi flows throughout the rainy season, normally at a depth of less than one metre, but usually dries out during the dry season when surface water can be found only in occasional pools. Sub-surface water is then obtainable by digging to a depth of about one metre into the sandy river bed. Baboon and warthog were seen to scoop out hollows in the river bed and so make water available to themselves and other animals.

The Black Umfolozi River has a perennial flow and, even though flow is much reduced during the dry season, is the only reliable water source in the Reserve. The survival of many wild animals would be doubtful were the Black Umfolozi to dry out completely during a dry season.

Agricultural malpractices in the catchment west of the Reserve, such as removal of the protective vegetation cover by over-grazing, that result in flash floods rather than in sustained year-round flow, could lead to drying out of the River. Any large increases in the amount of water abstracted upstream of the Reserve for irrigation purposes during the dry season would aggravate the water shortage.

The Black and White Umfolozi Rivers are both subject to sudden floods after rainstorms. Photo 16, taken in the Reserve by Mr D. Rowe-Rowe, illustrates a small flood on the White Umfolozi. Some idea of the terrible force attainable by flood waters is exemplified by the severe, unseasonal floods of July, 1963. Heavy rains started falling on 2 July, 1963, and continued until 4 July, on which day 281.5mm rainfall was recorded at Mpila. According to Mr I. Player (unpublished records of the Natal Parks Board) and Mr N. Steele (1968, pp 107-110), the White Umfolozi at Mahobosheni, normally about 50m wide when flooding, was 1.6 km wide and possibly over 15m deep. The Black Umfolozi rose more than 16m above its bed. Raging floodwaters flooded over the river banks and, according to Mr Steele, swept away hundreds of animals as well as about two thirds of the large Ficus sycamorus trees lining the banks of the Black Umfolozi. Huge trunks of F. sycamorus, larger than one metre in diameter and about 16m long, rest today near the River beds as testimony of the force of those floods. As a result of the floods the Black Umfolozi acquired and still retains a sandy bed whereas its bed was previously rocky (Vincent, 1970, p 9).

2.3. Geology

The most detailed available geological map of the area of the Reserve (Van Wyk, 1963) was, at a scale of 1:500,000, too small to show much detail. A new geological map at a scale of 1:50,000 was, therefore, produced for the purposes of this study. A copy of the new geological map is given in Appendix 1. Information for the map was obtained from field observations, and from aerial photographs supplied by the South African Trigonometrical Survey. The stratigraphic nomenclature used follows Du Toit (1956).

INSERT GEOLOGY MAP AT APPENDIX 1

2.3.1. Sedimentary rocks

Sedimentary rocks of the Cape and Karroo Systems are found in the Reserve. All sedimentary rocks in the Reserve have an almost horizontal stratification, or dip eastwards by a few degrees. The sedimentary rocks are described below in a sequence starting with the oldest strata and ending with the most recent.

2.3.1.1. Table Mountain Series

Distinctive pinkish to purple quartzites and sandstones of the Table Mountain Series of the Cape system are the oldest rock outcrop in the Reserve. They were seen only in the Mhlolokazana area where they abut as a 40m high scarp against the east bank of the White Umfolozi River (Photo 6).

2.3.1.2. Dwyka Series

Dwyka tillite of the Karroo System is the next oldest rock. Some undulating country between the Madlozi Stream and the western boundary is formed on the tillite. The tillite contains boulders, pebbles and angular fragments, of granite, sandstone, quartzite, gneiss and granodiorite ranging in size from 50 cm to 0.5 cm as well as finer debris. The tillite is blue-grey and weathers to yellow-brown.

2.3.1.3. Lower Eccä

Finely plated, easily weathered, black, Lower Eccä shale of the Karroo System is next in sequence. The shale occupies some lower-lying country in the Reserve including parts of the gently undulating Pliocene country in the Mphafa and Gqoyini catchments. The shale is mostly concealed by deep soils but is occasionally exposed, particularly in streambeds as in the Munywane Stream (Photo 9). Water percolates easily between joints in the finely plated shale. If the percolating water contains dissolved carbonate salts, a tufa of white, encrusting salts is deposited on the shale surface and between the joints when the water



Photo 17. Mduba Hill on the horizon has a terraced topography of scarplets, covered by a Closed Woodland, alternating with benches covered by an Open Woodland. Mduba is part of the Miocene Surface as is the well-grassed foreground, which is covered by Themeda Grassland. The white flowered tree in the foreground is Dombeya rotundifolia; behind it is tall Aloe marlothii. Chibilenyathi, 6.7.70.



Photo 18. Large boulders of Middle Ecca sandstone protrude on the rocky scarplets. A dark, Combretum apiculatum Closed Woodland grows on the scarplets. A pale, well grassed Open Woodland occupies the hill top and the soil covered bench which separates the two scarplets, and which extends into the foreground. Note the greener and denser foliage retained during a dry season by the Closed Woodland compared with the Open Woodland. Chibilenyathi, 4.7.70.

evaporates (Photo 9).

2.3.1.4. Middle Eccca

The Lower Eccca shale is overlain by the Middle Eccca beds which comprise a number of layers of white to grey sandstones interspersed by other sedimentary layers, including mudstones, brown shales, and glittering micaceous shales. Considerable variation in the sandstone texture, from fine particles to coarse grits and pebble inclusions, is often seen on examination of 50 or 100m² of almost any sandstone outcrop in the Reserve.

INSERT PHOTOS 17, 18

A terraced topography consisting of alternating scarplets and structural benches is formed out of the Middle Eccca beds (Photos 17, 18). The hard sandstone strata are more resistant to weathering and tend to persist as rocky, fissured scarplets, whilst the other softer strata weather more rapidly to leave gently sloping benches. When a more rapidly weathering, softer stratum undermines an overlying, harder stratum, boulders of the overlying stratum break off and litter the bench. A few small caves, as near Lubisana, are evidence of such undermining. The scarplets and benches run almost parallel to hill contours because the Middle Eccca beds have an almost horizontal stratification. Extensive tracts of terraced topography are found in the Mduba, Buthelezi and Gome areas in the southern half of the Reserve.

Better moisture conditions prevail on the sandstone outcrops and scarplets than on outcrops of other rock types in the Reserve. The Middle Eccca sandstones are one of the best aquifers in South Africa (Professor L. King, pers. com.). The better moisture conditions arise partly from water held in interstices, pores and crevices in the sandstone, and partly from more ephemeral moisture arising from rain, fog and dew that gathers on and trickles down the rock faces.

2.3.1.5. Stormberg sediments

The youngest sedimentary rocks found in the



Photo 19. During a drought period, a high water table is held on the upstream side (right) of this dolerite dyke (centre) which intrudes Lower Ecca shale, and a lower water table lies in the pool on the downstream side (left). See text for explanation. Note plant debris from plants lying trapped, about two metres above the streambed, in branches of an *Acacia robusta* sapling. Small plants of *Phragmites australis* grow at the water's edge. Munywane Stream, 23.7.68.



Photo 20. Shallow, stony soil typical of uplands is visible beyond the fence where farmland, outside of the Reserve, is heavily grazed by domestic livestock. The same soil extends into the foreground, within the Reserve, but is concealed by a dense stand of the *Themeda - Panicum* Community, which is lightly grazed by indigenous herbivores. An *Acacia tortilis* Open Woodland contains some leafless trees of *Sclerocarya caffra*; young *Acacia* spp. saplings invade the grass layer which is too sparse for burning beyond the fence. Fewer saplings occur in the periodically burned, dense grass stand in the foreground. Westwards view from the Miocene Surface at Khukho, 14.7.69.

Reserve are sandstone, shale and mudstones of the Stormberg Series. Their stratigraphy was not positively ascertained but they seem to be from the upper part of the Cave Sandstones. These rocks occupy country lying between Qaqualwempisi and the east boundary fence where they constitute a parallel series of low-lying ridges and intervening valleys (Photo 2).

2.3.2. Volcanic rocks

Volcanic rocks found in the Reserve include dolerites, basalt and rhyolite of the Karroo System. Only the more extensive outcrops of these rocks are shown on the geological map.

Numerous dolerites have intruded through the sedimentary strata. The dolerites crop out as extensive, almost horizontal sills covering up to 50 ha and more, as at Mbulunga, and as almost vertical dykes ranging from less than one metre thick to several metres thick. The dykes are so plentiful and of such universal distribution that they can be found in almost any 50 ha portion of the Reserve. The dolerite is a very fine grained, dark, homogeneous rock which on weathering forms almost spherical, red-brown boulders.

Although water is often held in shatter zones associated with dolerite dykes, unfragmented dolerite is impervious to the passage of water. Thus water movement through a sedimentary rock can be arrested at a barrier created by a dolerite dyke, and the water dams up behind the dyke. Photo 19 shows a higher water table contained on the upstream (right) side of a dolerite dyke than is contained in a pool on the downstream (left) side of the dyke. This photograph of the Munywane Stream was taken during the dry season and no surface flow was detected; surface flow being known only during and after rainstorms. Arrest of subterranean flow through sand in the streambed and through Lower Ecca shale, here intruded by the dyke, probably accounts for the pools of water. Subterranean water could well be stored against some of the dolerite dykes situated elsewhere in the Reserve.

INSERT PHOTO 19

The basalt was seen only on the summit of Ciyana Hill, at the south-east corner of the Reserve, where it caps underlying Stormberg sediments. The basalt is rather like dolerite in appearance, but contains many small white amygdales about one millimetre in diameter.

The rhyolite is also rather like the dolerite in appearance, but is light grey and contains a fair amount of quartz. The rhyolite outcrops in the form of acid dykes, of which only a few were found in the Reserve. The acid dykes are particularly resistant to weathering; they stand out above the surrounding country as narrow ridges, about five metres wide and a few metres high. The acid dykes are quite easily confused with the fault breccia described below.

2.3.3. Faulting

Several faults in the Reserve, of which only the longer ones are shown on the geology map, have displaced rock strata both laterally and vertically. Two of these faults warrant mention.

One long fault is aligned north-south along the Madlozi Valley. This is the most conspicuous fault in the Reserve because parts of its length are marked by a one to two metre wide outcrop of hard, grey, fault breccia that protrudes about one metre above the soil. Upward movement of land to the west of the Madlozi fault has brought the Table Mountain Series closer to the surface so that it is visible at Mhlolokazana; were it not for the fault and upward movement, the Table Mountain Series would have remained concealed at depth.

Another long fault runs along the western margin of Qaqualwempisi Hill near the south-east corner of the Reserve. Rock strata on the east of the fault have been displaced downwards so that the younger and stratigraphically higher rocks of the Stormberg Series are exposed, as on Qaqualwempisi and Ciyana. Older and stratigraphically lower rocks of the Beaufort Series, which lie in between the Ecca Series and the Stormberg Series, are concealed below the Stormberg Series in the south-east of the Reserve.

2.4. Soils

Table 1. A correlation of Woodland Communities and some soil, topographic and rock features in Umfolozi Game Reserve. Soil nomenclature after Van der Eyk, Macvicar and De Villiers, 1969.

	Woodland Community	Soil Series and (Form)	Topographic Site	Rock substrate
Upland Soil Association	Acacia caffra	shallow, stony soil	hilltops above 270m alt.	dolerite and sediments
	Acacia tortilis	shallow, stony soil Williamson (Gemvale)	hill tops and debris slopes hill tops	dolerite and sediments tillite
	Acacia burkei	Springfield (Clovelly)	pediments and benches	sandstone and quartzite
	Acacia nigrescens	- - (Kiaora)	hills and pediments below 145m	dolerite
	Mixed Combretum - Other spp.	Mispah (Mispah)	benches	Middle Ecca sediments
	Acacia nilotica	Arcadia (Arcadia)	pediments	shale
Soil Association	Acacia nilotica	Uitvlugt (Estcourt) Waldene (Longlands)	valley bottoms valley bottoms	shale tillite
	Acacia grandicornuta	Doveton, Makatini and Shorrocks, all of (Hutton)	alluvial terraces	various
	Spirostachys africana	Bonheim (Bonheim), Rensburg (Rensburg), Sun Valley (Shortlands)	stream banks	various
Riverine Association	Phoenix reclinata	coarse alluvium	stream beds	various
	Acacia robusta	fine alluvium	river banks	various

2.4.1. Introduction

Soils were investigated after the various woodland communities in the Reserve had been determined. Four stands from each of the woodland communities were selected for purposes of studying the soils. The four stands selected from each community were not situated in close proximity to each other within one region of the Reserve, but were widely separated in different parts of the Reserve, whether in the centre, or to the north, south, east or west. A stand was selected because it contained the dominant species of the community in question and seemed, to the author, to be typical of the community with regard to the other species present.

A soil pit was excavated at about the centre of each stand. Soil profiles shown in the pits were examined by Mr R. Ludorf, pedologist at Cedara College of Agriculture, who kindly identified the soils to soil form and, when possible, to soil series. Information from the soil pits was supplemented by many additional observations in streambanks, gulleys, and road cuttings, made initially by Mr Ludorf, and later by the author.

All of the soil forms and most of the soil series seen in the Reserve are also present in the Tugela Basin and have been defined and described by Van der Eyk, Macvicar and De Villiers (1969). Soil nomenclature and definitions used in this study are, therefore, taken from Van der Eyk et al (1969); but certain features such as soil depth and parent material are described from profiles seen in the Reserve. Chemical and mechanical analyses were not done on the soil profiles in the Reserve to confirm series identifications which should, therefore, be regarded as tentative.

Soils in the Reserve were found to be classifiable into one of three Soil Associations, either Upland, Bottomland or Riverine, depending on their topographic situation as explained in the relevant sections below.

INSERT TABLE 1

The soils could fairly easily be correlated with the woodland communities and the rock substrate, as well as with topographic situation, as is shown in Table 1. This Table serves as a summary when soil details are described below, and when relationships between the woodland communities and their habitats are described in Chapter 4.

A more detailed examination of the soil than was possible in the time available for this study would be needed for production of a soil map. However, some idea of the distribution of a particular soil form or series is obtainable by finding which woodland community is correlated in Table 1 with the particular soil, and then by observing the distribution of the woodland community on the vegetation map given at Appendix 1.

2.4.2. Upland Soil Association

Soils of the Upland Association are present in localities where water run-off drains away fairly rapidly, as on hill tops, hill sides, debris slopes and the structural benches of terraced topography.

The upland soils are usually stony, shallow at usually 50 cm and less deep, and leached (Photo 20). The soils have a low moisture storage capacity on account of their stony and shallow nature. Plants growing on the uplands experience, therefore, severe soil moisture stress during the dry, winter season, and can also experience drought during rainless spells that may be protracted for several weeks on end during the summer. The upland soils are so leached that Mr Ludorf (pers. com.) regards them as being infertile for agricultural purposes. The upland soils are developed in situ and bear a close resemblance to the underlying parent rock, but can be so shallow and immature, particularly on the Miocene Surface, that they cannot be named even at soil form level. Five upland soils are, however, identifiable where less shallow and stony conditions prevail, notably on the Pliocene Surface.

INSERT PHOTO 20

The Williamson Series is confined to those hills made of tillite which lie west of the Madlozi Stream. The Williamson Series has a very dark, grey brown, orthic A1 horizon over a cutanic B horizon containing over 30 percent clay (Van der Eyk et al., 1969).

The Arcadia Series is sometimes found developed over Lower and Middle Eccca shales. The shales weather rapidly and, for this reason, the Arcadia soils are often deeper than other upland soils. The Arcadia Series is a marginalitic soil having a calcareous, black, vertic A1 horizon that shows a high, greater than 40 percent, clay content, a very strong, fine angular blocky structure, and is fertile (Van der Eyk, et al., 1969). In the Reserve the A1 horizon usually lies directly on decomposing shale or micaceous shale; there is no B horizon.

A common soil of the Upland Association is a dark red or brown, as yet undescribed, series of the Kiaora soil Form which nearly always occurs in situ over dolerites. The Kiaora Form consists of a melanic A1 horizon overlying a red structural B (Van der Eyk et al., 1969). The undescribed series in the Reserve is usually less than 50 cm deep, contains much clay, and is mostly stony or bouldery. The undescribed series would closely approximate with the Kiaora Series described by Van der Eyk et al. (1969) were it not for the presence of a diffuse zone of minute carbonate particles found near the bottom of the B horizon. The presence of carbonate particles in a soil of the Kiaora Form is probably ascribable to low rainfall in the Reserve. A higher rainfall would have leached away excess carbonates.

A grey, loose, sandy soil of the Springfield Series develops in situ over sandstones and quartzites of the Table Mountain Series and over Middle Eccca sandstone. The Springfield Series has an orthic A1 horizon over a yellow apedal, non-calcareous B Horizon; the B horizon has a low, below 15 percent, clay content and consists mostly of sand (Van der Eyk, et al., 1969). This soil in the Reserve is highly water permeable. Water percolates rapidly through the A and B horizons which are consequently highly leached and infertile. Some of the leached materials are deposited as a coating on the surface of the sandstone bedrock underlying the soil, where yellow and grey colorations indicate temporary



Photo 21. An advanced stage of sheet erosion. typical of Hutton Form soils on alluvial terraces. The horizontally spread roots of Acacia grandicornuta Closed Woodland are confined to the A horizon, and do not penetrate the B horizon. Note the many, large, white carbonate nodules exposed in the B horizon in the foreground. Carbonate nodules are typical of bottomland soils. Mfulamkhulu, 10.5.70.



Photo 22. A ten metre deep profile of Hutton Form soils is exposed in the distant stream bank, cut through an alluvial terrace. No surface flow is visible on the sandy stream bed (foreground), which is partly stabilised by a Riverine Woodland and by reedbeds. A large tree of Acacia robusta is on the left; reedbeds, and palms of Phoenix reclinata, are across the middle distance. Muniwane Stream, 23.7.68.

waterlogging during the rainy season. During the dry season the soil is very dry.

The fifth identifiable soil of the Upland Association, the Mispah Series, is found on the structural benches of terraced topography where it develops from a mixture of parent materials, mostly of Middle Eccia shale but also including some sandstone and some dolerite. The Mispah Series has a very dark, grey brown orthic Al horizon that is low in bases, strongly acid and infertile (Van der Eyk et al., 1969). In the Reserve the Al horizon is stony, rarely exceeds 30 cm in depth, and overlies a very stony rubbish horizon consisting of fragments of the parent rocks.

2.4.3. Bottomland Soil Association

Soils of the Bottomland Association are present in localities where water run-off drains away more slowly or tends to accumulate on valley bottoms, on alluvial terraces, and on the toe-slopes of pediments where the pediment slope gradually merges into a valley bottom. The bottomland soils are from one to several metres deep, and are illuviated as shown by an accumulation of many large carbonate nodules, two or three centimetres in diameter, in their B horizons (Photos 14, 21). The bottomland soils are, therefore, said by Mr Ludorf (pers. com.) to be highly fertile for agricultural purposes. Stones are rare, but the easily erodible B horizons are hard and impenetrable to plant roots (Photos 9, 14, 21). The bottomland soils have a much higher moisture storage capacity than the upland soils, and remain fairly moist even during rainless spells in summer. But the bottomland soils do dry out during winter and plants then experience a severe soil moisture deficiency.

INSERT PHOTO 21

Soils in the bottomlands of the Reserve have higher carbonate concentrations than are described by Van der Eyk et al. (1969) for occurrences of the same series in the Tugela Basin. The extraordinarily high carbonate content of the bottomland soils in the Reserve is probably ascribable to a highly seasonal, low, 635mm mean annual rainfall which is

insufficient for leaching away excess carbonate salts. During the dry season when the soil dries out, the excess carbonates are precipitated, and the carbonate nodules gradually increase in size and number as the years of low rainfall pass by.

Eight soil series described below constitute the Bottomland Association. The soils are of transported origin and are not, therefore, derived from the underlying rocks.

The Waldene Series is of minor occurrence, being confined to bottomlands in the tillite country west of the Madlozi Stream. The Series is derived from transported tillite; has a very dark, grey brown, orthic A1 horizon; a perched gley containing from 15 to 35 percent clay and fine sand; and a soft, plinthic B horizon (Van der Eyk et al., 1969). The soil is badly eroded near drainage lines.

The Uitvlugt Series is described by Van der Eyk et al. (1969) as a duplex soil having a dark grey brown, loamy sand, orthic A1 horizon with a clay content below 15 percent; the A1 rests on a perched gley, having a clay content above 30 percent, which in turn rests on a prismatic, textural B horizon. Some extensive gullies are forming in this soil, as in the Mphafa catchment. Once the rather sandy, protective topsoil has been removed, as in game paths or vehicle tracks, the exposed B horizon erodes very rapidly. Waterlogging is evident for one or two days after heavy rainfall when many shallow puddles of water remain in small depressions at the soil surface. The B horizon is very hard and is impenetrable to plant roots which are confined to the A horizon. The hard B horizon is evidently also impermeable to water and seems responsible for the waterlogging by preventing internal drainage of the soil.

Texturally variable soils are found along streambanks which include soil mosaics containing several different series, of which the Bonheim, Rensburg and Sun Valley are the more common. All the soils along and near streambanks are badly eroded (Photos 9, 10, 14).

The Bonheim Series has a melanic A1 horizon, with more than 35 percent clay, which overlies a dark brown, structured, highly calcerous B horizon. The Rensburg Series has a dark grey to black, vertic A1 that overlies a firm gley

which is calcerous in the upper part. The Sun Valley Series has an orthic A1 resting on a red, calcerous, structured B horizon containing 35 percent, and more, clay (Van der Eyk et al., 1969).

The alluvial terraces of the Quaternary Surface are covered by distinctive orange and red tinted soils. The soils are the Doveton, Makatini and Shorrocks Series of the Hutton Form. They all possess an orthic A1 horizon over a red, apedal B horizon. Water easily infiltrates the A horizon and easily penetrates the B horizon. Clay content in the B horizon of these soils varies from 15 to 35 percent in the Shorrocks Series, from 35 to 55 percent in the Doveton Series, and from 35 to over 55 percent in the Makatini Series. (Van der Eyk et al., 1969).

INSERT PHOTO 22

Soils of the Hutton Form can be very deep, even up to ten metres (Photo 22), and are, according to Mr Ludorf (pers.com.), the most fertile of all soils in the Reserve. Depletion of the grass cover through over-grazing as well as trampling of the soil surface by animals and by vehicle wheels, have resulted in much gully and sheet erosion. Erosion reveals the numerous, large carbonate nodules responsible for the exceptionally high soil fertility (Photo 21). Another peculiar feature of the Hutton soils is an occasional inclusion of boulder beds. Beds of boulders, ranging from a few centimetres to one metre in diameter, worn smooth by water action mark channels previously occupied by rivers and streams.

2.4.4. Riverine Soil Association

Unconsolidated alluvia up to five and more metres deep constitute the Riverine Association. The alluvia are unstable and fairly easily stripped away by flood waters, but are less easily eroded where stabilised by reedbeds and other vegetation (Photos 4, 12, 22).

A fine alluvium, consisting of mixed sands and silt, is confined to the beds and banks of the Black and White Umfolozi Rivers, and to the surrounds of the larger pans that lie close to the Rivers.

A coarse alluvium consisting of water rounded boulders and pebbles, of sand and silt, is found in parts of the beds of the streams, notably the Munywane, Fuyeni and Mphafa Streams. This alluvium has accumulated to a significant extent only at the confluences of the streams with the White Umfolozi River, and extends from the confluences for distances of about one or two kilometres up the lower reaches of the streams. The boulders are deposited in a stream bed near the confluence apparently as a result of a reduction in the velocity of stream flood waters, which tend to bank up against the mainstream of flood waters in the River.

Plenty of soil moisture is available throughout the year to plants growing on the alluvia, whether as open water during the rainy season or as water contained just below the alluvial surface during the dry season. Plant communities growing on the alluvia are, therefore, the only communities in the Reserve which do not suffer a severe soil moisture deficiency during the dry season.

2.5. Climate

2.5.1. Introduction

The climatic year in the Reserve is divisible into two seasons, a moist summer which extends from October to March inclusive, and a dry winter from April to September inclusive. Seasons of spring and autumn for the vegetation differ somewhat from year to year because of an erratic rainfall distribution. Vegetational spring can commence in September, October or November, depending on when the first heavy rains of the climatic year are recorded; autumn can start in April or May, depending on when rainfall tails off and when the effects of drought are shown by the vegetation.

2.5.2. Insolation

No records for insolation are available for any area within or near the Reserve. The closest comparable locality for which adequate records are available is Estcourt in Natal. Estcourt is 70 km south of the Reserve and 120 km farther inland (Fig.1), and lies at an altitude about 890m higher than the Reserve. Although winter temperatures at

Table 2. The intensity of insolation at noon, expressed as a percentage of the maximum possible noon insolation, expected on level ground, on north and on south aspect slopes of several gradients in Umfolozi Game Reserve. Obtained from data supplied by Schulze (1970) for a latitude of 28° 30' south.

Slope		Percent maximum possible noon insolation			
Gradient	Aspect	October 1	December 22	April 1	June 21
0°	-	89.4	99.8	87.3	62.2
10°	N	96.0	99.8	94.7	75.0
	S	82.0	97.0	78.0	49.0
20°	N	99.6	96.6	98.8	85.2
	S	68.0	90.7	65.5	34.0
30°	N	99.8	90.7	100.0	93.0
	S	57.0	83.0	52.3	21.0
40°	N	96.0	82.0	98.7	98.1
	S	44.0	71.4	38.0	10.0
Summer				Winter	

Estcourt are much lower, the summer temperatures and the mean annual rainfall (750mm) are fairly similar to the summer temperatures and the rainfall (635mm) at Mpila in the Reserve. It is likely that insolation conditions at Estcourt are comparable with those at Mpila.

According to Reynolds (1963, p 7) the longest hours of mean daily bright sunshine are recorded at Estcourt for winter months of June (8.66 hr), July (8.57 hr), and August (8.45 hr); whilst the lowest hours of mean daily bright sunshine are recorded for summer months of December (6.76 hr), January (6.81 hr), February (6.80 hr) and March (6.78 hr). Slightly longer hours of mean daily bright sunshine could be expected in the Reserve than at Estcourt. Overcast skies are probably less frequent in the Reserve which receives 115mm less mean annual rainfall than Estcourt. A highest daylight duration of just over 14 hrs in midsummer (December 22nd), and a lowest duration of just over 10 hrs in midwinter (June 21st), are possible for the Reserve (List, 1951, pp 508, 520).

INSERT TABLE 2

Different intensities of insolation, depending on aspect, gradient and time of year, are received by the various slopes in the Reserve. An idea of some differences in the intensity of noon insolation expected in the Reserve on north and south aspect slopes of 10, 20, 30 and 40 degrees and on level ground, is given in Table 2. The intensity of noon insolation is expressed as a percentage of the maximum possible insolation at noon on the following four days. October 1st which is taken as the beginning of summer in the Reserve; December 22nd which is mid-summersday, the southern solstice and the longest day in the southern hemisphere; April 1st which is taken as the beginning of winter in the Reserve; and June 21st which is mid-wintersday, the northern solstice and the shortest day in the southern hemisphere. The insolation data apply to latitude $28^{\circ}30'$ south, which passes 7.5 km south of the Reserve, and were obtained from Schulze (1970). Mr R. Schulze kindly checked the data for accuracy.

Table 3. Air temperatures at Mpila for the periods April 1960 to March 1963 and September 1966 to September 1970.

		Air Temperatures °C												
		O	N	D	J	F	M	A	M	J	J	A	S	Year
Maximum														
Absolute		39.4	40.0	40.0	43.3	40.0	40.0	36.7	34.4	31.7	33.3	40.6	38.9	43.3
Mean		28.4	29.4	30.7	32.6	32.9	29.9	27.6	26.7	25.3	25.3	26.8	26.8	28.7
Minimum														
Absolute		10.6	10.0	13.3	16.7	8.3	6.7	10.6	8.9	7.2	6.7	8.9	10.0	6.7
Mean		18.2	18.5	19.9	21.8	21.6	20.3	17.4	15.7	13.2	13.2	14.8	17.3	17.6
Mean		23.3	23.9	25.3	27.2	27.2	25.1	22.5	21.2	19.3	19.3	20.8	22.1	23.2
Mean daily range		10.2	10.9	10.8	10.8	11.3	9.6	10.2	11.0	12.1	12.1	12.0	9.5	11.1
		Summer							Winter					

Table 2 shows for all of the days that north aspects can receive a higher insolation intensity at noon than south aspects of the same gradient. The differences in insolation intensity are least when the gradients are closer to the horizontal; e.g. on December 22nd a 10 degree north aspect can receive 99.8 percent of the maximum possible, and a 10 degree south aspect can receive 97.0 percent. But the differences are greater on steeper slopes, e.g. on December 22nd a 40 degree north aspect can receive 82.0 percent, and a 40 degree south aspect can receive 71.4 percent of the maximum possible. The differences are not so marked in mid-summer when the sun is nearly overhead at noon; but are very marked in midwinter when the sun is lower to the horizon at noon, e.g. on June 21st a 40 degree north aspect can receive 98.1 percent, and a 40 degree south aspect can receive less than 10 percent of the possible maximum. Nearly vertical south and south east aspect scarps in the Reserve, as at Momfu, Mpila and Nqabaneni, receive no direct insolation during midwinter.

West aspect slopes in the Reserve receive greater amounts of insolation than east aspect slopes. East aspects are partially protected from intense insolation effects by early morning fogs, or by a relatively moist morning air which filters out some of the heat rays, so that they receive less severe insolation than west aspects. West aspects are not protected in this way to the same extent. Much of the atmospheric moisture is lost later in the day as the atmosphere warms up, and west aspects are more strongly insolated in the afternoon when a greater proportion of heat rays are permitted to reach the ground.

2.5.3. Temperature

A summary of temperatures recorded over seven years at Mpila Camp, altitude 290m, is given in Table 3.

INSERT TABLE 3/

Mean monthly temperatures at Mpila are fairly steady throughout the year. They range from 23.3°C to 27.2°C

during summer, and from 19.3°C to 22.5°C in winter. Mean daily temperature range shows, on the average, that summer night temperatures are between 9.6°C and 11.3°C cooler than day temperatures; whilst winter night temperatures are cooler by between 9.5°C and 12.1°C than day temperatures.

Mean monthly maxima at Mpila did not fall below 28.4°C in summer, nor below 25.3°C in winter. The absolute maximum temperature measured over the seven year period of the records was 43.3°C . Absolute maximum temperatures did not fall below 39.4°C for any summer month, nor below 31.7°C for any winter month.

Mean monthly minima did not fall below 18.2°C in summer, nor below 13.2°C in winter. The lowest absolute minimum temperature recorded at Mpila is 6.7°C .

Greater temperature extremes than those shown above for Mpila have, however, been recorded at other lower lying places in the Reserve.

For instance, a screen temperature of 45°C was recorded by Mr N. Owen-Smith (pers. com.) at Madlozi, altitude 244m, on October 16th, 1969. This temperature exceeds the absolute maximum of 43.3°C recorded at Mpila. October is not usually the warmest month of the year, so even higher temperatures than 45°C are possible in January and February which are normally the warmest months.

Absolute maxima recorded at Tobothi Camp, altitude 183m, over the inclusive period from June to November, 1968, were about 3°C higher on most days than corresponding temperatures recorded at Mpila, altitude 290m. The difference in altitude between the two stations is only 107m. Temperature lapse rate could therefore, under standard atmospheric conditions, account for only about 0.7°C of the 3°C temperature difference (List, 1951, p 268). Some other factor as well as difference in altitude is, therefore, involved: the weather station at Mpila is on almost level ground, but Tobothi Camp is on a west aspect slope. It seems, therefore, that temperatures higher than those recorded at Mpila are probable on west aspect slopes, as at Tobothi, Mhlolokazana and Makhamisa, as a result of the stronger insolation expected on west aspects.

On the other hand, absolute minima recorded at Tobothi in June and July, 1968, were about 3°C lower on most

days than corresponding temperatures at Mpila. The lower minima at Tobothi in June and July were probably due to temperature inversions at night when cold air flowed down the Black Umfolozi and other valleys. Vincent (1970, p 10) writes: "In the winter, frost may occur in the lower lying country. Several definite records have been found of visible frost - one in May, 1916, in the White Umfolozi valley, another in 1952, and several since then." As neither frost nor near freezing temperatures have been recorded at Mpila, the occurrence of frost seems restricted to the lower lying parts of the Reserve, as on the Quaternary Surface, where cold air collects at times of temperature inversion.

Were sufficient records available, temperature extremes in the Reserve would likely be found to range from freezing point, or slightly lower, to more than 45°C .

2.5.4. Wind

Little information, apart from a few casual observations, is available on wind in the Reserve. Very strong or gale force winds were not noticed during the course of this study. Only a few wind-blown trees were seen fallen in widely separated localities, and the majority of these were already dead before being toppled by the wind. A greater number of wind-blown trees would have been expected were very strong winds a usual climatic feature. Breezes and light winds were most often detected.

North-west and west winds blow at times, for a day or two, particularly during August, September and October. These winds are often hot and dry. For instance, at Tobothi Camp a maximum temperature of 23.3°C was recorded on September 26th, 1968, which was a clear, still day. But on the following two days whilst a hot, dry, west wind was blowing, maxima of 31.7°C and 37.8°C were recorded. Vapour pressure deficits measured at 0700 hr increased from four millibars on September 26th to 10 mb on the 27th, and to 10.7 mb on the 28th. The hot, dry west wind continued to blow during the night of September 27th, when an even higher vapour pressure deficit of 39.3 mb was recorded at 1940 hr even though the sun had set. Yet warmer and drier conditions are probable on some afternoons, when the strongest intensity of

Table 4. Monthly rainfall and number of rainy days at Mpila for the period January 1959 to September 1970.

	O	N	D	J	F	M	A	M	J	J	A	S	Year
Rainfall in millimetres													
Maximum	196.8	204.4	143.5	219.8	147.4	222.5	118.6	76.0	86.5	325.3	58.0	66.0	914.4 (1963)
Minimum	32.4	45.6	32.1	19.5	10.3	12.0	9.5	0(2 yr)	0(3 yr)	0(2 yr)	0(1 yr)	6.1	479.4 (1959)
Mean	76.1	98.6	62.0	81.5	51.7	87.8	51.2	20.7	24.4	32.6	17.9	30.9	635.4
Number of rainy days													
Maximum	12.0	15.0	18.0	14.0	13.0	13.0	11.0	7.0	5.0	6.0	9.0	7.0	93 (1960)
Minimum	5.0	6.0	4.0	4.0	3.0	3.0	3.0	0	0	0	0	2.0	59 (1965)
Mean	8.5	10.3	9.3	8.2	7.2	7.0	5.7	2.6	2.0	2.2	2.8	4.2	70.5
Summer								Winter					

insolation is received, while hot, dry, west winds are blowing.

In summer, south winds are the chief rain bearing winds. Such winds are sometimes accompanied by a sharp drop in temperature, to the order of about 10°C , often noticeable within the hour. For example, a maximum temperature of 31.1°C recorded on November 9th, 1968, which was an overcast, still day, fell to 22.3°C on November 10th, a rainy day of south winds. During winter, south winds rarely bring rain unless cool, overcast and gusty conditions persist for several days at a time. A light drizzle may then fall.

Cooling breezes were more frequently experienced on the higher, more exposed parts of the Reserve than on the lower lying, less exposed parts. Sometimes when breezes were felt on hill tops, as at Mpila, calmer air was experienced on low ground near the White Umfolozi River.

2.5.5. Precipitation

INSERT TABLE 4

Almost twelve years of rainfall records taken at Mpila, altitude 290m, are summarised in Table 4. The mean annual rainfall is 635.4mm. This amount is considerably less than the following means supplied by the South African Weather Bureau (Anon; 1965, pp 116, 182) for neighbouring stations outside the Reserve. Hlabisa, only 19 km north west of Mpila at an altitude of 512m, receives 1126.4mm mean annual rainfall. Dukuduku, 37 km east of Mpila at 70m altitude, receives 989.2mm. Empangeni, 47 km south of Mpila at 137m altitude, receives 1108.2mm. Mahlabatini, 38 km north west of Mpila at 843m altitude receives 802.0mm. The Reserve is, therefore, regarded as a comparatively dry enclave within Zululand.

About 72 percent of the mean annual rainfall in the Reserve falls during the summer rainy season from October to March inclusive. The remaining 28 percent is distributed over the winter months, which constitute a dry season from April until the end of September. The rainy and dry



Photo 23. A fog is seen at dawn to conceal the low lying, Quaternary Surface including the White Umfolozi River. Higher ground of the Pliocene Surface is visible along the horizon above the fog. In the foreground, many leaves are retained by Combretum apiculatum (left and right), whilst few leaves are retained by Dombeya rotundifolia (centre). Makhamisa, 5.7.70.



Photo 24. Widely spaced, flat crowned trees of Acacia tortilis dominate an A. tortilis Open Woodland. In the foreground to the right are A. nilotica (shorter tree) and A. gerrardii (taller tree). A few forbs and Acacia spp. seedlings indicate that the dense grass cover of the Themeda Community had not been burned in the preceding three to five years. The gently rolling to flat Miocene Surface of Ngqolothi. 14.7.69.

seasons are not strictly bound by these months owing to a rather erratic rainfall distribution evident from a comparison in Table 4 of the maximum and minimum rainfalls for each month.

Monthly rainfall decreases from the end of March and occasionally no rain may fall in the months from May to August inclusive. June and July are normally the driest months. For example, in 1959 the amounts of zero and 23mm respectively were recorded; in 1962 zero and five mm; and in 1968 the amounts of zero, 2.4 and 3.1 mm were respectively recorded for May, June and July.

The mean rainfall of 32.6 mm shown for July in Table 4 is much higher than the five or ten millimetres normally received, and arises from a most exceptional rainfall of 325.3mm in July, 1963. On July 4th alone a deluge of 281.5mm was recorded; such a heavy rainstorm for the Reserve being without precedent in living memory. The next highest rainfall noted in the Reserve for any single day is 123.4mm recorded on December 25th, 1960.

Infrequent hailstorms occur about once in two years. They contribute little moisture and are not known to have damaged the vegetation to any significant extent.

INSERT PHOTO 23

Fog, mist and particularly dew are probably important moisture sources for the vegetation during the dry season.

Fog is fairly common in winter as an opaque, white blanket covering the lower valleys (Photo 23). Fog settles during the night into the valleys as a result of cold air drainage. At dawn, most of the Reserve lying below about 180m altitude, including the Quaternary Surface, is concealed by the fog which gradually lifts. All or most visible traces of the fog have vanished by 0900 hr.

Light and isolated patches of mist, of short duration, occur mostly on some summer evenings.

On some summer and many winter nights, a dense dew wets rock faces, dampens the uppermost soil particles, and coats plants so that droplets of water are seen to cover

Table 5. Monthly evaporation in a Symons Pan at Hluhluwe Dam for the period 1st October, 1963 to 31st December, 1970. Data supplied by Mr R.T. Rudd, Department of Water Affairs.

Evaporation in millimetres													
	O	N	D	J	F	M	A	M	J	J	A	S	Year
Maximum	177.0	185.7	214.6	236.5	204.5	192.8	140.0	122.7	102.6	115.3	132.6	175.5	236.5
Minimum	143.0	124.5	175.5	168.4	128.0	125.2	108.0	88.4	78.2	84.6	101.1	131.3	78.2
Mean	154.9	156.2	193.8	201.2	170.2	163.3	119.9	103.4	92.2	96.5	120.4	146.8	1718.8
Summer								Winter					

their leaves and stems.

All 38 grasses, shrubs, trees and ferns tested by Gallwey (1956) were found to absorb water droplets directly through the cuticle of both upper and lower leaf surfaces, irrespective of whether specialised cells, such as stomata, were present. The rate of absorption was found to be slow, from one to five hours, but Gallwey (1956) concluded that water deposited on leaves from fog and dew was probably of importance to the plants.

The plants tested by Gallwey (1956) included several species present in the Reserve, such as Bothriochloa insculpta, Panicum maximum, Themeda triandra, Trichilia emetica, Xeromphus rudis and Ficus capensis. Many plants in the Reserve probably benefit from moisture absorbed from fog, mist and dew.

Lightning often accompanies summer rain storms in the Reserve. Ranger M. Astrup (pers. com.) recollects two lightning fires in the Reserve over the last four years, but these burned only a few hectares before being extinguished by subsequent rain. The one fire was started on Zintunzini in October, 1969, when a bolt of lightning was seen to strike the ground.

2.5.0. Evaporation and humidity

The nearest station to the Reserve for which evaporation data are available is Hluhluwe Dam, altitude 81m, situated 30 km north east of Mpila. The vegetation surrounding the Dam is similar to that on the low lying, Quaternary Surface of the Reserve. A mean annual rainfall of 646.9mm at the Dam is similar to the 635.4mm in the Reserve.

INSERT TABLE 5

Seven years of evaporation records from Hluhluwe Dam kindly provided by Mr R. T. Rudd, Department of Water Affairs (pers.com) are summarised in Table 5. Mean evaporation in summer is 1039.6mm and in winter is 679.2mm. The highest maxima of 236 and 204mm are recorded for January and February, which are the warmest months in the Reserve.

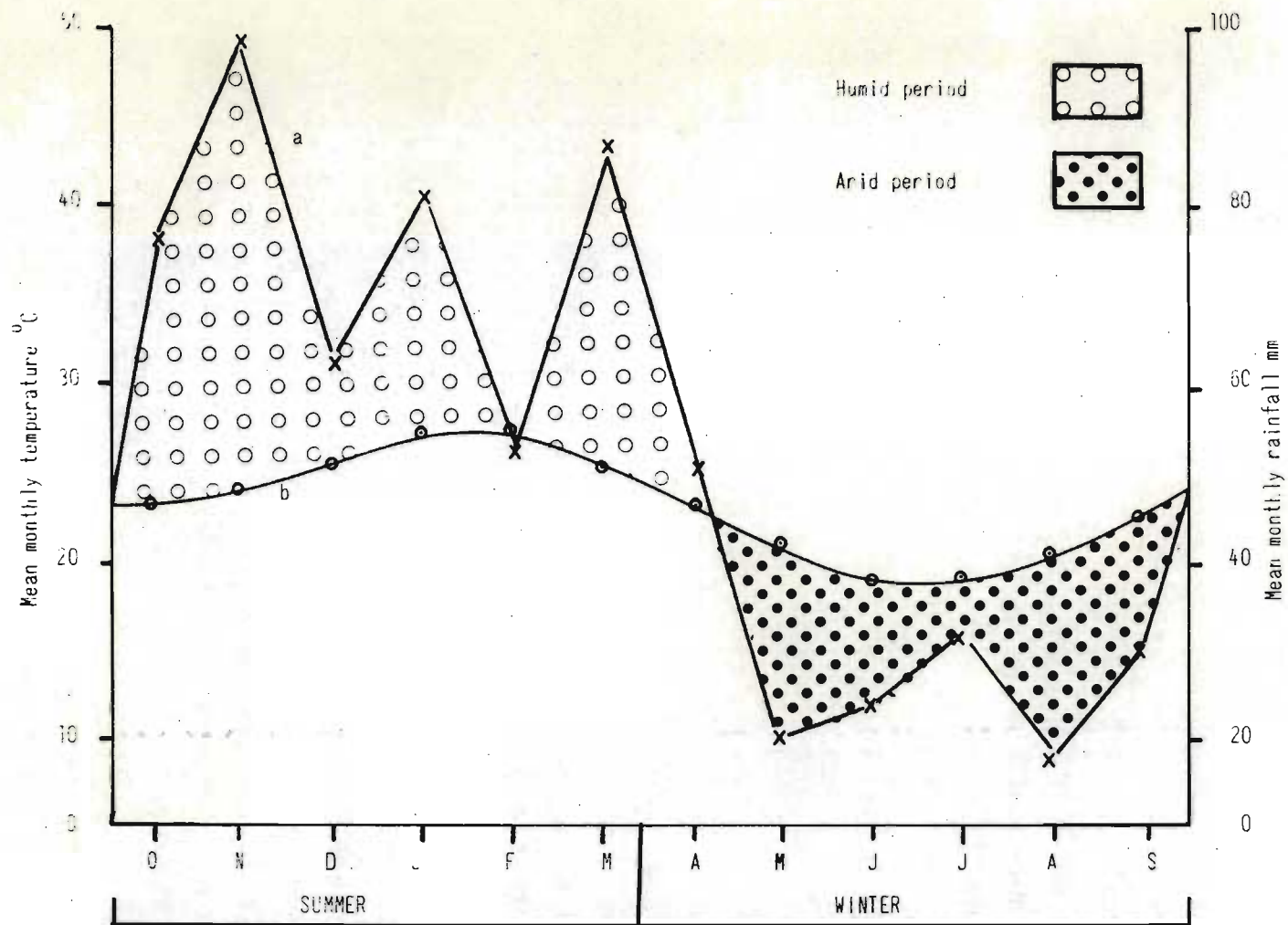


Fig. 2. A climatic diagram for Umfolozi Game Reserve constructed by plotting mean monthly rainfall (a) and mean monthly temperature (b) to show humid and arid periods. Constructed after Walter, 1963.

The ratio of evaporation to rainfall at the Dam is 2.7 : 1. A similar ratio would likely apply for most of the Reserve, where a ratio of evaporation to rainfall of 2.3 : 1 could then be expected for summer, and 3.8 : 1 for winter.

A dry, sub-humid to nearly semi-arid climate is thus indicated for the Reserve, and is reflected by the predominantly deciduous, mostly Acacia spp. dominated, woodlands present. The broader climatic features of the Reserve approximately fit the CB'w climatic category of Thornthwaite as described by Schulze (1947). The CB'w category refers to a sub-humid, warm mesothermal climate distinguished by moisture deficiency during winter.

INSERT FIG. 2

The duration and intensity of humid and arid periods is portrayed in Figure 2, which is a climatic diagram for the Reserve constructed after the method of Walter (1963). In the climatic diagram, mean temperature and mean rainfall recorded at Mpila are plotted for each month; the same units of length are used on the vertical axes for 10°C temperature and for 20mm rainfall. According to Walter (1963), a humid period is interpreted in Figure 2 for the summer, where the rainfall curve (a) rises above the temperature curve (b), and an arid period for the winter, where the rainfall curve falls below the temperature curve. The size of the vertical interval between the two curves portrays the intensity of humid or arid conditions. The intensity of humid and arid conditions in the Reserve is, however, not so accurately portrayed in Figure 2; the twelve year period of rainfall records available being too short to produce a smooth, precise mean rainfall curve because of the erratic rainfall distribution. For instance, somewhat less arid conditions than are usually expected are shown for July because the exceptionally high rainfall of 325mm for July, 1963, is included amongst the values used for determining the twelve year mean.

The arid period of winter is a limiting factor for plant development. Most trees and many shrubs shed their

leaves during winter. The aerial portions of plants, whether trees, shrubs or grasses, but excluding succulents, are mostly dormant in winter. Arid conditions are intensified towards the end of winter, in August, September and October, when the hot, dry, west winds blow - and particularly so when the early summer rains are delayed. Vegetation growing on soils of the Upland and Bottomland Associations also experience a severe soil moisture stress towards the end of winter when soil moisture levels are lowest. Some moisture is, however, available to vegetation growing on soils of the Riverine Association; but the alluvial moisture seems somewhat inadequate for overcoming arid atmospheric conditions in winter because most trees growing on the alluvia are deciduous to a greater or lesser extent.

The most arid of all conditions in the Reserve are encountered on west and north-west aspects, which receive the strong afternoon insolation, and where the highest temperatures are consequently recorded. For example, a temperature of 36.8°C and a vapour pressure deficit of 44 mb were recorded on the north west aspect scarp at Mhlolokazana on 13th March, 1971, at 1600 hr. A lower temperature of 32.9°C and a lower vapour pressure deficit of 32 mb were simultaneously recorded on an east aspect at the same altitude at Mhlolokazana. A far higher proportion of drought resistant, succulent plants are found on west and north west aspects than on other aspects in the Reserve. North aspects are also rather dry, although not quite as dry as the north west aspects. North and west aspects in the Reserve are, therefore, included as xeroclines. Comparatively cooler and moister, south and east aspects, exposed to lesser intensities of insolation, are included as mesoclines. The most mesic conditions are on south east aspects which receive the least insolation. Tree and shrub densities are usually denser on south east aspects compared with other aspects.

* * * * *

CHAPTER THREE

VEGETATION METHODS AND RESULTS

3.1. Vegetation physiognomic categories

3.1.1. Procedures

The main physiognomic categories of vegetation in the Reserve were recognised by examining, in the field and on airphotos, the features of tree density and tree crown diameter. Five categories were distinguished as follows: A Grassland containing few or no trees; an Open Woodland containing widely spaced trees; a Closed Woodland with such a high tree density that the crowns were in contact, or almost so; a Mixed Woodland containing both Open and Closed stands; and a Riverine Woodland where trees were irregularly spaced, but where crown diameters were about two times larger than in the other categories.

The vegetation was then examined in finer detail in the field in order to obtain some physiognomic details on the tree, shrub and ground layers composing the physiognomic categories.

Dr D. Rogers of Augustana College and formerly of Wisconsin University, U.S.A., and the author attempted to determine tree density from a few selected stands in the Reserve. Twenty point-centred quarters were laid out in each stand, and the distances were measured from each point-centre to the nearest tree in each quarter. The distance data were processed according to the method of Cottam and Curtis (1956) in order to determine tree density. The results were, however, thought by the author to present a misleading picture for reasons mentioned in the discussion (Chapter 6.4.1.3.); and the results are, therefore, not presented. A qualitative description of tree density, as seen from the airphotos and in the field, is given instead. The qualitative description of density is, however, supplemented by some measurements taken in a manner described below.

Some measurements were taken of tree height, tree crown diameter, and inter-crown distances in the categories of Open, Closed, and Riverine Woodland. For these purposes, five representative stands were selected from each of the three

Table 6. Tree height, crown diameter, and inter-crown distance in selected stands from Physiognomic categories of Open, Closed, and Riverine Woodland. Data given in metres and based on fifty trees taken from each of fifteen stands.

	Physiognomic categories								
	Open Woodland			Closed Woodland			Riverine Woodland		
	Height	Crown diameter	Inter-crown distance	Height	Crown diameter	Inter-crown distance	Height	Crown diameter	Inter-Crown distance
Mean values per stand in metres	5.0	3.7	8.5	8.5	6.0	0.1	16.9	8.2	39.8
	5.4	5.2	16.7	7.7	4.2	0.9	18.3	10.3	72.4
	8.1	5.3	15.0	6.3	4.0	0.5	16.1	11.7	45.7
	5.2	4.8	40.0	6.8	7.2	6.8	15.4	12.6	60.2
	5.8	5.8	113.3	5.7	4.4	5.5	15.0	9.0	42.9
Mean for each category in metres	5.9	5.0	38.7	7.0	5.2	2.8	16.3	10.4	52.2

categories. A traverse was conveniently laid out in each stand by following a road, a game trail, stream or river bank. The nearest trees on either or both sides of the traverse were selected for measurement, and the traverse was ended after 50 trees had been measured. Tree height was estimated by comparison against an eight foot (2.44m) long ranging rod, divided into one foot (0.30m) units, held vertically against the tree trunk. The vertical projection of the crown diameter on the ground was recorded by use of a steel tape measure. The longest and shortest diameters were both measured, and the mean diameter calculated, when the vertical projection of the crown was noticeably irregular. The distances separating the crowns of neighbouring trees were measured by use of the steel tape measure.

INSERT TABLE 6

Mean values for the measurements of the trees are given for each stand in Table 6, and the mean values for each physiognomic category, corrected to one decimal place, are also given. The mean values of tree height and of crown diameter given are reasonably consistent between the five stands from each category. The mean values of tree height, as well as of crown diameter, from the five stands can, therefore, be safely combined into a single mean value for the category as a whole; and the single mean value is incorporated when the category is defined below. But the mean values of inter-crown distance vary considerably between the stands within a category, and the combination of these values into a single mean is liable to be misleading. The range of inter-crown distances most often encountered in a physiognomic category, as determined by looking over the original measurements, is given rather than the mean value when the category is defined.

3.1.2. Definitions of Grassland and Woodland

The physiognomic categories in the Reserve are defined by using to a large extent some of the diagnostic criteria proposed by Phillips (1971) for the physiognomic classification of vegetation types in South Africa.

Grassland is defined as a dense community consisting almost entirely of grasses, but including some associated forbs and a few sedges (Photo 12). The grasses are mostly tall, from 50 to 100 cm high, perennial species having a rather coarse, bunched or tussocky habit. Very few, or no, trees and shrubs are present excepting in some areas where the Grassland is being invaded by young woody plants.

Woodland is used here in a generic sense to replace the old, and often loosely applied term Savanna. However, Phillips' (1971) usage of Woodland in a specific sense was found not entirely suitable for use in the Reserve, where Woodland is retained as a generic term to include the following variants present.

INSERT PHOTO 24

Open Woodland (equivalent to the Open Woodland of Phillips, 1971) is a park-like community of trees and shrubs which rise above a dense grass layer (Photos 2, 24). Tree density is rather variable; the tree crowns are most often widely separated, from about 15 to 60m and occasionally more, but can be closer where occasional aggregations of two or three neighbouring trees can be in contact, or almost so. The trees are of medium, about six metres, height but are taller at eight metres where Acacia nigrescens is dominant. The trees have flat-topped or irregularly shaped crowns, about five metres in diameter, and are mostly of spinescent Acacia spp. having finely divided, compound leaves and a thick, ridged or flakey bark. A few shrubs are inconspicuous in the Open Woodland because they are less numerous than the trees and, at a height of about three metres, are also shorter. A dense ground cover of grasses, physiognomically similar to the grasses contained in the Grassland, extends throughout the Open Woodland. The grasses are grazed short, to less than 50 cm, in some areas of Open Woodland.

Tree density in Open Woodland varies somewhat depending on topographic location and aspect. The trees tend to be more widely spaced on level ground and on xeroclines, and are more closely spaced on mesoclines, particularly on south-east aspects where density can increase to the extent that the Open Woodland approaches a Closed Woodland condition.



Photo 25. An impenetrable, long-established, thicket of spinescent Acacia luederitzii. A fairly dense grass stand of Panicum maximum grows protected from grazing at the periphery of the A. luederitzii crowns; but a heavily grazed Panicum coloratum Community, too sparse for burning, lies unprotected in the foreground. Pliocene Surface near Gqoyini Stream, 8.5.70.



Photo 26. A Mixed Woodland comprises the dense Bush Clump, formed by closely growing trees and shrubs, and the surrounding Open Woodland. The figure stands in a narrow, one to two metre wide, zone of heavily grazed grasses which surrounds and protects the Bush Clump from passing fires. A Pliocene pediment at Madlozi, 9.5.70.

Closed Woodland (equivalent to the Woodland of Phillips, 1971) contains dense tree and shrub communities underlain by a poorly developed ground layer of grasses and forbs. The tree crowns can be in contact, or lightly overlap, or can be spaced by about 10m and more apart (Photos 2, 8, 27). The trees are of medium height, at about seven metres, and have rounded, rather than flat topped or irregularly shaped crowns, about five metres in diameter. Some typically spinescent Acacia spp. as well as other, unarmed tree species are present. The unarmed species are also characterised by a thick bark; some have simple, undivided leaves (e.g. Spirostachys africana, Sideroxylon inerme, Pappea capensis) whilst others have compound leaves (e.g. Schotia brachypetala, Commiphora spp.). A conspicuous shrub stratum, from three to five metres tall, is present. The shrubs can be widely spaced, from 10 to 20m apart, or can grow so densely that their crowns overlap and intergrow to form a Thicket. A sparse ground layer consisting of a few, short, less than 50 cm, pioneer grasses and of several forb species is characteristic of the Closed Woodland; but taller and denser islands of grasses are found where protected from grazing at the periphery of woody plants.

Thicket refers to a scrubby, dense growth of woody vegetation, mostly of shrubs or short species, up to five metres tall but also including some taller trees (Photo 25). The woody plant stems tend to be spindly and often so closely spaced that adjacent crowns inter-grow. The term Thicket is preferred by Phillips (1971) as an alternative to Scrub because Thicket better describes the tangled growth habit, and has a wider international usage. Most Thickets in the Reserve are, evidently, secondary derivations of Closed Woodland that develop when the number of woody plants increase as a result of over-grazing and an absence of fire. Thicket growth can be so dense that the ground layer of grasses and forbs is shaded out.

INSERT PHOTOS 25, 26

Mixed Open/Closed Woodland, abbreviated to Mixed Woodland, is the term used when stands of Closed Woodland,



Photo 27. During the dry season a sluggish, low water flow runs from the background down the sandy bed of the White Umfolozi River. Reedbeds stabilise parts of the sandy banks. Large, dark-toned and widely spaced trees (mostly Acacia robusta) of Riverine Woodland occupy the sandy slip-off banks beyond the reach of most floods. A lawn-like growth of the Cynodon Community covers the sand between the large trees. Smaller, pale-toned and more closely spaced trees of Acacia grandicornuta Closed Woodland occupy a fairly level alluvial terrace which extends outwards from beyond the Riverine Woodland. South-east view from Momfu, 7.5.70.

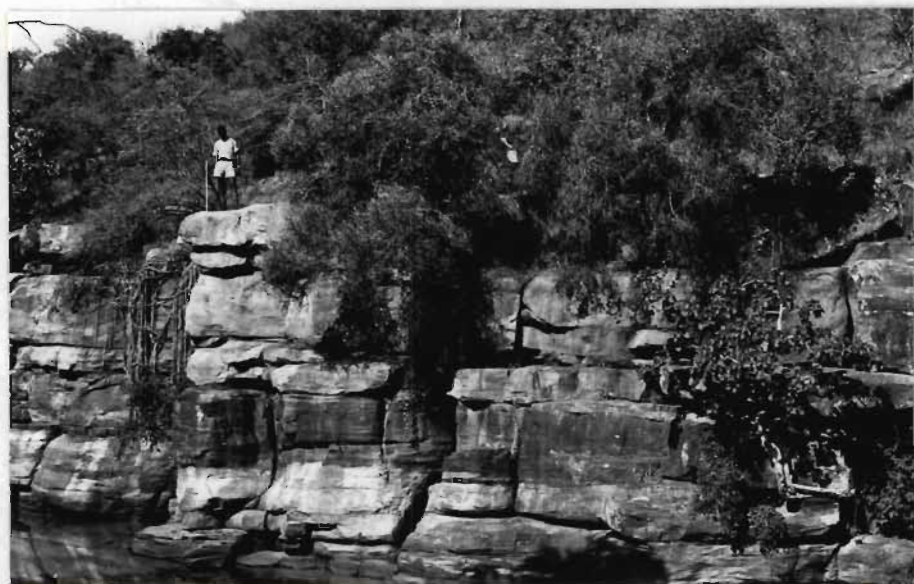


Photo 28. Some pioneer plants colonise crevices in Middle Ecca sandstone. Succulent, trailing stems of Cissus quadrangularis are at the left hand; and succulent bushes of Euphorbia tirucalli are at the centre. Ficus soldanella (right) has roots firmly lodged in crevices; the roots go down to a pool of water at the foot of the rock face. North aspect of a Quaternary gorge below Mphafa Waterhole, 10.5.70.

including occasional stands of derived Thicket, and of Open Woodland occur as the parts of a physiognomic mosaic. The mosaic can have a regular pattern, as found on the areas of terraced topography where bands of Closed Woodland growing on scarplets alternate with bands of Open Woodland growing on benches (Photo 13). Or the mosaic can be rather disordered, as when small, up to 50m diameter, almost circular stands of Closed Woodland are scattered irregularly within a larger stand of Open Woodland. The almost circular stands of Closed Woodland are also known as Bush Clumps (Photo 26). The Mixed Woodland shows some physiognomic similarity with the Transition Woodland/Open Woodland described by Phillips (1971) to have developed through human agency, but this is not the case in the Reserve where Mixed Woodland has developed independently of human activity.

INSERT PHOTO 27

Riverine Woodland consists of large, tall, up to 17m, trees, some shrubs and a patchy ground layer of grasses (Photo 27). The tree density varies considerably within a stand; some neighbouring trees being aggregated into clusters so that their crowns are in contact, whilst others may be separated by as much as 60 or 100m. The tree crowns are rounded or irregular in shape, and are broad at about 10m in diameter. Palms, about five metres tall, are rarely present either in groves or as widely scattered individuals. Large, five metre tall, shrubs grow in open areas between the trees, but rarely grow in dense shade beneath the trees. A discontinuous ground layer, alternating with bare patches, occupies part of the sandy substrate and can extend into the shade beneath the trees. Coarse, rank grasses and fine, short stoloniferous grasses are present. The tree canopy of Riverine Woodland in the Reserve is generally so open that this category cannot be included as the Riverine Forest defined by Phillips (1971).

3.2. Delineation of landscape units

The Reserve, as seen on airphotos, was delineated

into 531 discrete landscape units for purposes of facilitating vegetation sampling and mapping. The following criteria were used for delineation of the landscape units and are listed below in order of importance:

- (a) Vegetation physiognomy, whether a Grassland, an Open, Closed, Mixed or Riverine Woodland was present;
- (b) Changes in landform shown by a break in topographic gradient, whether the landform was a hill top, scarp, debris slope, pediment, or bottomland;
- (c) Marked changes in aspect, whether a north, south, east, or west, aspect was present;
- (d) Changes seen in photo tone due to rock or soil features of the substrate.

Delineation was done by examining the airphotos, taken in 1960 at a scale of 1:40,000, through a stereoscope. The boundaries of the landscape units were delineated, in ink, on the airphotos such that the landscape contained within any one unit appeared to be homogeneous with regard to the criteria listed above. The position as to where a boundary line should be drawn could often not be exactly determined as, for instance, when attempting to decide where the boundary should lie between a north aspect and an east aspect when both aspects were part of the same hill. In such an instance, the boundary position was determined by reference to one of the other criteria listed above; and the boundary could be drawn where, for example, some difference was seen in slope gradient or in vegetation.

The annotated airphotos were taken into the field and checked for accuracy against actual conditions on the ground. The procedure of landscape unit delineation was then repeated on a clean set of airphotos so that any inconsistencies could be reduced as far as possible, and to take advantage of an improvement in the operator's photo-interpretative ability gained through additional knowledge of ground conditions. The landscape units were numbered, from one to 531, in ink on the airphotos so that every individual

landscape unit could be readily identified.

3.3. Procedure for woody plants

3.3.1. Introduction

It was decided to treat the woody vegetation separately from the grasses as somewhat different techniques would be needed on account of their different properties. The woody vegetation was investigated first because the woody plants were more obvious than the grasses, were initially better known to the author, and seemed to reflect the broader, more stable features of the environment, such as soil condition, rather than the finer, more dynamic features of biotic activity largely reflected by the ground layer of grasses.

Species percentage constancy, being a quantitative measure of vegetation, was chosen for describing the social status of the various plants composing the communities. Species percentage constancy, also known as species percentage frequency, was chosen because it can be calculated from species presence -and- absence records which are easily and rapidly obtainable in the field (Brown, 1959, pp 26-33). The choice of a quantitative measure dependent on easily and rapidly obtainable field data was a prime consideration in view of the considerable effort and time required to enumerate communities in the large, 49,280 ha area of the Reserve.

3.3.2. Sampling

Field investigation suggested that one vegetation sample taken from each landscape unit, i.e. a total of 531 samples, might well be adequate for obtaining sufficient sample data from the woody vegetation for the following reasons. Firstly, that the 531 samples would be distributed in all sections of the Reserve, and would likely include representative portions of all landscape or environmental features present, whether of vegetation, soil, or micro-climate. Secondly, the woody plant composition seemed fairly uniform, but with some variation, within a landscape unit. The degree of uniformity could, of course, not be ascertained with much certainty until much later, when

quantitative data became available on community composition. However, the apparent dominant or dominants were present in most parts of a landscape unit. It seemed logical, therefore, to use a total of 531 samples and to distribute the samples by locating one in each landscape unit.

A plotless sampling technique, based on the point-centred quarter method of Cottam and Curtis (1956) was chosen for obtaining woody species presence records from the landscape units. The plotless technique, which provided the same amount of information content from every landscape unit irrespective of differences in woody plant density, was preferred in view of the wide range of woody plant densities embraced by the several Woodland categories present. By contrast, use of a quadrat or other kind of plot would have included many more plants when a sample was taken from a Closed Woodland, and far fewer plants when taken from an Open Woodland. The plotless technique was also preferred because errors due to edge effect are precluded, whereas use of a plot introduces an edge effect.

A pilot sampling experiment was conducted to gauge what number of point-centred quarters might generally be suitable for obtaining a record of species presence in a landscape unit. For this purpose fifteen representative landscape units were chosen at convenience, five being chosen from each category of Open, Closed, and Riverine, Woodland. A traverse was laid out in a landscape unit by starting at any convenient point, usually near the margin of the landscape unit, and by pacing out a distance of 750 paces in a direction more or less parallel with the widest diameter or length of the landscape unit as shown on the airphoto. Direction was maintained by looking at a distant landmark, such as a hill or a large tree.

A first centre point was placed at the start of a traverse, and two axes were scratched on the ground through the point. One axis was in the direction of the traverse, and the other perpendicular to the direction of the traverse. Each axis extended for about one pace in both directions from the point centre such that the four quarters or quadrants of a circle could be visualised. The axes dividing off the four

Table 7. The cumulative number of species encountered through use of 15 point-centred quarters in each of fifteen samples taken in Open, Closed and Riverine Woodland. Mean values are shown as whole numbers.

Sample		Number of point-centred quarters														
Woodland category	No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Open Woodland	1	3	5	7	8	8	10	10	10	12	12	14	14	15	16	16
	2	3	3	3	4	5	9	9	10	13	13	13	15	15	15	15
	3	4	7	11	11	11	12	12	12	13	14	15	15	15	15	15
	4	4	6	7	7	9	9	10	10	11	11	11	12	13	13	13
	5	4	8	9	9	10	11	13	14	15	15	15	15	16	17	17
Closed Woodland	6	4	5	6	9	12	12	12	15	15	16	16	17	17	18	18
	7	4	8	11	13	15	15	16	17	19	19	19	19	19	20	20
	8	3	8	10	12	12	13	14	14	16	17	17	17	17	18	19
	9	4	7	10	11	12	13	13	13	13	14	15	15	16	17	18
	10	4	6	8	11	12	15	17	17	17	17	17	17	17	18	18
Riverine Woodland	11	4	6	9	12	12	12	12	12	12	14	14	14	14	14	14
	12	3	5	6	7	8	8	9	10	10	10	11	12	12	12	12
	13	4	6	7	8	9	9	9	10	10	10	10	10	11	11	11
	14	4	5	6	7	8	9	9	9	9	9	9	9	10	10	10
	15	2	6	6	6	8	9	9	9	9	10	11	11	12	13	13
Total		54	91	116	135	151	166	174	182	194	201	207	212	220	227	229
Mean		4	6	8	9	10	11	12	12	13	13	14	14	15	15	15
Cumulative number of species encountered																

quarters were imagined to extend indefinitely so that the circle diameter could be of any size, provided it was sufficiently large to include at least one woody plant in each of the quarters. The nearest tree or shrub to the centre point in each quarter was recorded as being "present". Only plants having a stem diameter equal to three centimetres or more at breast height were recorded. Multi-stemmed plants were recorded if their stems were judged to have a total diameter of three centimetres or more at breast height. Measurements of plant height, stem girth, crown dimensions, and other such quantitative measurements usually taken through employment of the point-centred quarter method, were not taken because information was sought only on species presence.

The remaining 14 centre points were set out at 50 pace intervals along the traverse, and the nearest tree or shrub species present in each quarter was recorded as present in the same way as done at the first centre point. The fifty pace interval was increased in some Open Woodland stands, where the plants were very widely spaced, so as to avoid sampling the same plant more than once.

INSERT TABLE 7

The results of the pilot sampling experiment are given in Table 7, which shows the cumulative number of species encountered by the fifteen point-centred quarters taken from the fifteen landscape units. The mean numbers of species encountered by the point-centred quarters from all fifteen of the landscape units are also shown.

Table 7 shows an increase in the mean cumulative number of species, from four to 15, encountered by an increase in the number of point-centred quarters from one through to 15. The least number of species, from 10 to 14, are encountered by samples taken from the Riverine Woodland, and the largest number, from 18 to 20, are in the Closed Woodland; whilst an intermediate number, from 13 to 17, are encountered in the Open Woodland. The rates of increase differ somewhat between samples taken from the three Woodland

categories, and also differ between the samples taken from within one Woodland category. However, more than one half of the total number of species recorded by a sample is encountered before the seventh point-centred quarter is included. An average increase of only four additional species is obtained by more than doubling the number of point-centred quarters from six to 15. A sample consisting of six point-centred quarters seemed, therefore, to generally provide an economical and adequate record of species presence in a landscape unit. The apparent dominants, and other seemingly important species, in a landscape unit had been included in a sample after the sixth point-centred quarter had been taken; and so the number of six point-centred quarters was chosen as a suitable sample size. It was decided not to vary this sample size to take into account the variations in floristic richness, shown by the three Woodland categories, because an equal amount of information content was required of all samples.

Trees and shrubs in the Reserve were then sampled by means of six point-centred quarters, set out at fifty paces intervals (or more in some Open Woodland stands) along a traverse in each landscape unit. Only 516 of the 531 landscape units were, in fact, sampled. The remainder of 15 landscape units were on inaccessible scarps and were not sampled because it was physically impossible to do so. Sampling was done over the period from June to December, 1968. During the earlier part of this period the leaves of many plants had fallen, and when the identification of a species was, in the absence of flowers, dependent on leaf character, it was not always possible to identify the species beyond genus level. Thus certain species of Commiphora, Diospyros, Grewia, Strychnos and Rhus were identified only at genus level. At least 109 tree and shrub species were encountered by the $24 \times 516 = 12,384$ plant records constituting the samples.

One field sheet was allocated per landscape unit for notation of habitat and vegetation data. The habitat data recorded were an estimate of slope gradient, any visible features of the substrate such as soil drainage,

depth, colour, stoniness, and kind of rock outcrop. In addition, details of altitude and aspect were obtained from the 1: 50,000 Topography Map with contours marked at 50 ft (almost 15m) intervals, located at Appendix 1.

3.3.3. Analysis and mapping

The normal association-analysis method, abbreviated to normal analysis, of Williams and Lambert (1959, 1960) was chosen for analysis of the sample data. Normal analysis was chosen because it can be used towards the production of a vegetation classification, and towards the production of some quantitative floristic data on plant communities. Normal analysis was also chosen because it makes use of the simple, species presence-and-absence records as were obtained through sampling of the woody vegetation in the Reserve. Some other, more sophisticated analytical methods, such as ordination techniques (see McIntosh, 1967), were not chosen because they depend on supplies of strictly quantitative sample data, such as density, cover, or "indices of importance" (see Curtis and McIntosh, 1951), which were not sampled in the Reserve. Computer facilities were easily available for normal analysis, which had already been shown by Grunow (1967) to be effective for the classification of some woodland communities in South Africa.

The woody vegetation sample data for each of the sampled 516 landscape units were entered on punch cards. Percentage frequency values for the 109 species recorded by the 516 samples were calculated by use of an IBM 1130 digital computer. Of the 109 species, some 45 were found to have a frequency of less than one percent. These 45 rarer species were excluded from further computation as their inclusion would unlikely affect the results of normal analysis (see Webb, Tracey, Williams and Lance, 1967), but would considerably increase the duration and expense of computation.

The population of 516 samples, embracing the 64 retained species, was then computed for normal analysis by following the instructions of Williams and Lambert (1959, 1960). Computation required twelve hours. The parameter

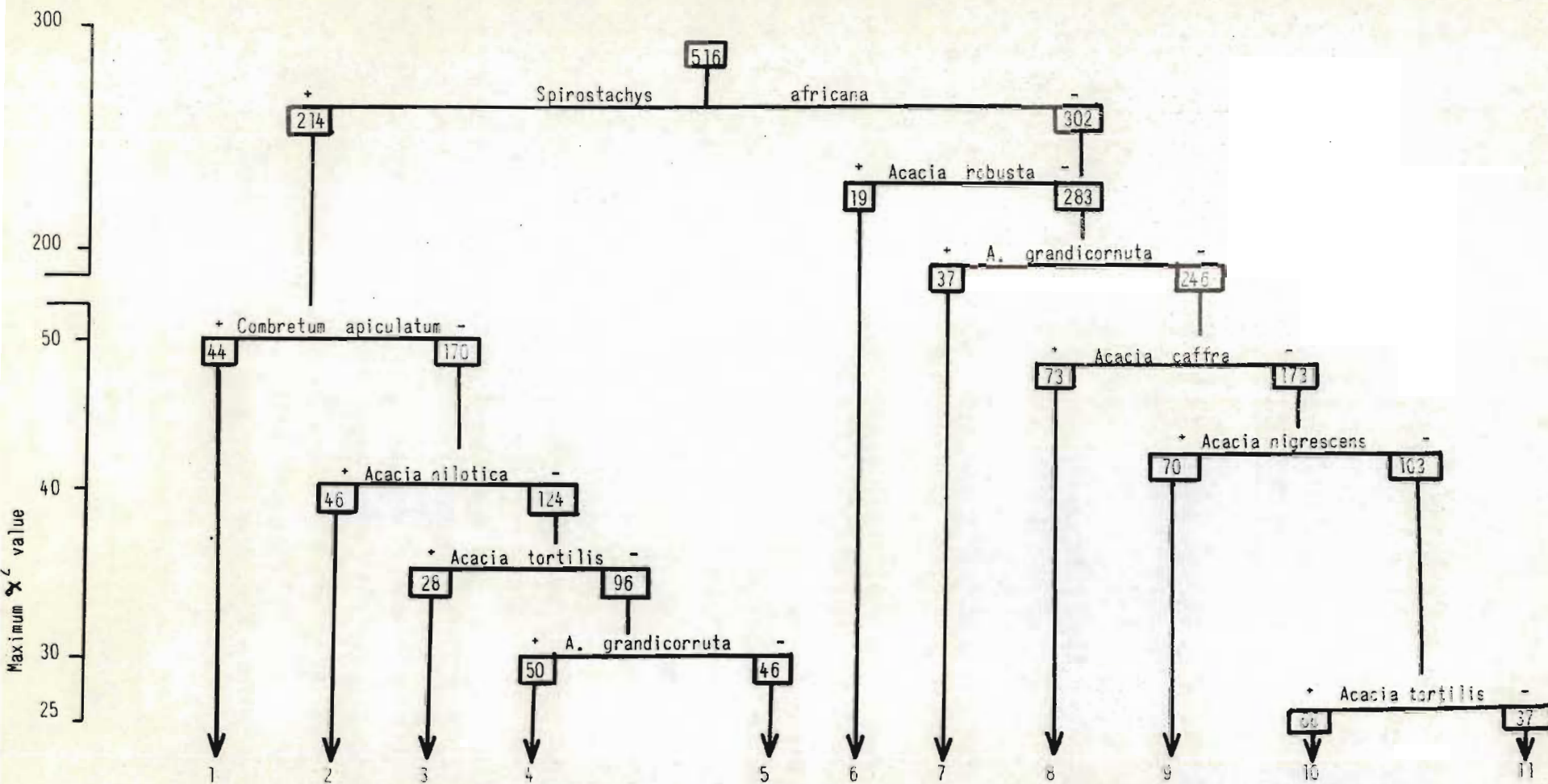


Fig. 3. Classification of 516 samples of woody plants into eleven groups of samples by normal analysis. See text.

used for measuring association between species was χ^2 with Yates's correction. The subdivision parameter used was the highest $\sum \left[\frac{\chi^2}{N} \right]$ but in this parameter uncorrected χ^2 values were used. Subdivision was terminated either when the number of samples comprising a group of samples was 15 or less, or when the highest, single χ^2 value in a group was equal to 3.841, depending on whichever event occurred first.

INSERT FIG. 3

The normal analysis of the 516 samples resulted in a hierarchical classification of the samples into eleven discrete groups of samples as shown in Fig. 3. The species upon which the classification, or subdivision, of a group depended is written at the relevant position in the Figure. The number of samples, either containing that species as present (+) or as not containing that species (-), comprising a group of samples is written within a rectangular enclosure. The maximum χ^2 association value encountered within any one group of samples can be read off the graduated scale on the left hand margin of Fig. 3; this is done by finding the point on the scale which is at the same level as the uppermost margin of the rectangular enclosure for the group in question.

The various steps taken during the normal analysis were as follows. During normal analysis the parent population of 516 samples was hierarchically divided, and further subdivided as shown in Fig. 3, into increasingly more homogeneous and smaller groups of samples, so that association between the species within groups was progressively reduced. Subdivision of the parent population, containing 516 samples, into the first two smaller daughter groups containing 214 and 302 samples respectively, was done in the following way. Association between all possible pairs of species contained in the 516 samples of the parent population was calculated in two -by -two contingency tables. Both positive and negative χ^2 values for each species were summed together, irrespective of whether the values were positive or negative. Spirostachys africana was found to have the highest value of $\sum \left[\frac{\chi^2}{N} \right]$ amongst all the other species. All

samples containing S. africana as present, totalling 214 in number, were then divided off into the positive daughter group; and the remaining 302 samples of the parent population, which did not contain S. africana as present, were divided off into the negative daughter group shown in Fig. 3.

Species associations within the two daughter groups, and in subsequent daughter groups, were examined in the same way as above, and the process of hierarchical classification and subdivision was repeated until a final stage when 60 daughter groups had been produced. Subdivision was terminated at the final stage, also known as the long-division level, either because further subdivision of any group would have reduced the number of samples in a daughter group to below the minimum number of 15 prescribed, or because no further significant species associations were detected. A later field evaluation of the results of normal analysis showed, however, that the classification was not intelligible at the long-division level of 60 groups, but was intelligible at a higher level of 11 groups, known as the short-division level. The classification in Fig. 3 is, therefore, given only as far as the short-division level shown by the eleven groups. Normal analysis thus resulted in a classification of the parent sample population into eleven groups according to the species they did, or did not, contain.

At each subdivision, the computer print-out listed the following information:

- (a) the single species on which the subdivision was effected;
- (b) the quantity of samples classified into each of the two, resultant daughter groups, as well as the identity numbers of the samples according to the landscape units where they were obtained;
- (c) the quantity of samples containing each species as being present;
- (d) the highest single χ^2 value (with Yates's correction) in each daughter group; and a list of the sums of χ^2 (uncorrected).

Quantitative floristic data on species percentage constancy and species percentage fidelity were calculated in the following ways for each of the eleven groups by using some of the print-out information listed above. The percentage constancy value (C) for every species in a group was calculated by the formula $C = \frac{n}{N} \times 100$, where n = the number of samples in the group containing the species, and N = the total number of samples constituting the group. The percentage fidelity value (S) for every species in a group was calculated by the formula $S = \frac{n}{P} \times 100$, where n = the number of samples in the group containing the species, and P = the total number of all samples containing the species. The quantitative floristic data were entered onto tables.

A first vegetation map was drawn in the following way. A transparent overlay was placed over a mosaic of the annotated airphotos. The boundaries of the landscape units shown on the airphotos were traced on the overlay. The identification number of each landscape unit, corresponding with the identification number of the woody vegetation sample taken from the landscape unit, was also written on the overlay. A particular colour code was chosen to represent each of the eleven groups. Each of the sampled landscape units was coloured-in according as to which particular group, out of the eleven possible, its woody vegetation sample was classified by the normal analysis.

3.3.4. Evaluation of results

The results of the normal analysis, including the classification shown in Fig. 3, the tables giving species percentage constancy and percentage fidelity, and the vegetation map, were taken into the field for evaluation and interpretation.

The eleven final groups, shown in Fig. 3, were found on evaluation to correspond more or less with the main woody plant communities in the Reserve. The classification shown in Fig. 3 seemed, therefore, to be a reasonably accurate classification of the woody communities; but several amendments to the classification, as outlined below, seemed desirable.

The 28 samples of Group 3 in Fig. 3 could not be

distinguished in the field from the samples of Group 6 apart from occasional trees of Spirostachys africana present in Group 3. Retention of Group 3 as a separate entity from Group 6 could not, therefore, be justified; and the 28 samples constituting Group 3 were re-allocated to Group 6.

The 37 samples of Group 7 were found to be ecological representatives of Group 4. The samples of Group 7 were taken from landscape units situated adjacent to landscape units represented by the samples of Group 7. An absence of Spirostachys africana from Group 7 was, in the circumstances, believed to be of little significance, and the 37 samples of Group 7 were re-allocated to Group 4 because Acacia grandicornuta was the dominant species in both Groups.

Apart from the re-allocation of the $28 + 37 = 65$ samples mentioned above, another 43 samples were found on field evaluation to have been misclassified into groups where they poorly fitted. The 43 samples had been misclassified owing to the fortuitous inclusion in a sample of one or two individual plants which were not so characteristic of the community to which the sample rightfully belonged, but which were more characteristic of some other community. The 43 misclassified samples were re-allocated to their correct groups by inspection. The nine groups of samples were found, after application of the amendments described above, to correspond with the nine main woody plant communities in the Reserve. Quantitative data in the form of species percentage constancy (C) and species fidelity (S) were then recalculated for the re-constituted, amended groups. These data are given in Tables 20 to 28 when the relevant communities are described in later sections. Those species having a constancy of less than 10 percent make an insignificant contribution to the communities and are omitted from the tables for purposes of brevity.

INSERT VEGETATION MAP AT APPENDIX I

The distribution of the communities is portrayed in a final vegetation map which was drawn after the classification was amended. The map was produced by transposing the

landscape unit boundaries from the airphotos to a base map at a scale of 1:50,000. A radial line plotter was used for transposing the boundaries. The following South Africa 1:50,000 sheets issued by the Government Printer, Pretoria, were used for the base map: 2831 : BA, BB, BC, BD. Each sampled landscape unit on the vegetation map was marked according to the community into which its woody vegetation was classified after the results of the normal analysis were amended.

3.3.5. Plant social status

Although dominance was not directly estimated through sampling of crown dimensions, stem diameter, or density, a visual assessment indicated that the tree having the highest percentage constancy in a community was also the dominant, constituting the bulk of the uppermost or main stratum canopy. The most constant and, therefore, dominant tree was also the same as that species on which the community was finally segregated during the normal analysis (Fig.3). Each community has, then, been named according to the single, dominant and most constant species. By so doing the diagnostic value and identity of the single species finally used for segregation and classification of the community is given maximum emphasis.

Braun-Blanquet (1932, p 53) has used percentage constancy as an expression of the "degree of presence" of a species in a community. The following five degrees of presence, proposed by Braun-Blanquet (*loc.cit.*), will be used when describing the contribution made by a species to a community. Summaries will be given at the foot of the tables showing the quantitative composition of the main woody communities. Each summary will state the quantity of species encountered for each degree of presence on the following basis.

- 5 = constantly present (in 80 to 100 percent of the stands).
- 4 = mostly present (in 60 to 79 percent of the stands).
- 3 = often present (in 40 to 59 percent of the stands).

2 = seldom present (in 20 to 39 percent of the stands).

1 = rare (in 1 to 19 percent of the stands).

In addition, the following five degrees of fidelity, also based on Braun-Blanquet (1932, p 59) will be used when describing the fidelity of a species to a community. A numerical range of fidelity values for the five degrees of fidelity was not given by Braun-Blanquet (1932), so the fidelity values quoted below were assigned by the author.

A. Characteristic species

Fidelity 5. Exclusive species : species completely or almost completely confined to one community (fidelity from 80 to 100 percent).

Fidelity 4. Selective species : species found most frequently in a certain community but also, though rarely, in other communities (fidelity from 60 to 79 percent).

Fidelity 3. Preferential species : species present in several communities more or less abundantly but predominantly or with better fidelity in one certain community (fidelity from 40 to 59 percent).

B. Companions

Fidelity 2. Indifferent species : species without pronounced affinities for any community (fidelity from 20 to 39 percent).

C. Accidentals

Fidelity 1. Strange species : species that are rare and are accidental intruders from another plant community (fidelity from 1 to 19 percent).

3.4. Procedure for grasses

3.4.1. Introduction

A main purpose of this study was to survey the vegetation with reference to its capacity to support the associated grazing animals. Since the larger, 6,558 kg/km²

Table 8. The cumulative number of grass species, encountered with twofold increases in size of quadrat area, detected from ten stands.

Stand No.	Cumulative number of species						
	Quadrat area in square metres						
	1	2	4	8	16	32	64
1	7	9	9	10	12	20	21
2	2	3	4	5	6	8	9
3	2	2	3	4	4	6	9
4	2	2	3	4	4	7	7
5	1	2	3	4	5	8	9
6	2	4	8	8	8	13	14
7	2	2	2	3	4	6	7
8	2	5	5	8	8	10	13
9	6	8	9	9	9	10	12
10	5	5	5	7	8	11	11
Mean	3.1	4.2	5.1	6.2	6.8	9.9	11.2

proportion of the total, 7008 kg/km² large herbivore biomass (Table 29) consists of animals almost entirely dependent on a grass diet, examination of the ground layer was concentrated mainly on the grasses themselves, and less attention was given to forbs.

It was decided to describe the grass communities on a basis of species percentage constancy because the species presence -and-absence records, required for determining percentage constancy, are more easily obtained than the kinds of data required for describing mass, density, volume, or some other absolute vegetation measure. It was also decided to classify the communities by the method of normal analysis (Williams and Lambert, 1959, 1960), and to identify the communities according to their dominant grasses. The reaction of the communities to grazing would be investigated by measuring grass height and by estimating percentage grass canopy cover. The intensity of grazing pressure would be assessed by noting the proportion of defoliated grasses, grass vigour and the proportion of bare ground.

3.4.2. Sampling

A preliminary reconnaissance was made so as to obtain an idea of the main grass communities present. A sample size suitable for sampling grass presence was then estimated in the following way.

Ten stands of grasses were selected as being representative of the main grass communities evidently present. A plot measuring two metres wide by 32m long, divided into 64 one square metre quadrats, was marked out at a convenient position in each stand. The perimeter of a quadrat was demarcated by twine stretched between wooden pegs, which were driven into the ground at each corner of the quadrat. The grass species in each quadrat were recorded as being present provided a stem of the species was rooted within the quadrat perimeter.

INSERT TABLE 8

The cumulative number of species encountered with every twofold increase in quadrat area, from one square metre to 64 m², is summarised for each plot in Table 8. Most of

the species in a plot are encountered by a quadrat area of 32m^2 ; a twofold increase in quadrat area to 64m^2 did not result in any species increment in stands 4 and 10, and resulted in small increases, from one to three species, in the other stands. A quadrat area of 32m^2 seemed, therefore, suitable for sampling species presence. However, the time of two or three hours needed for investigation of grasses in an area of 32m^2 was excessive in view of the limited time available for studying grasses in the large area of the Reserve. A smaller quadrat area of 16m^2 was chosen as being more practical, even though the mean number of 6.8 species recorded by areas of 16m^2 was less than the 9.9 species recorded by areas of 32m^2 . The quadrat area of 16m^2 was regarded to provide an adequate, representative sample because the dominant, and other evidently important grasses, had been encountered by the even smaller quadrats of eight square metres in area.

A circular plot of area 16m^2 and radius 2.26m was chosen in preference to a rectangular quadrat of area 16m^2 because a circular plot has a shorter perimeter than a quadrat of similar area; edge effect in the plot would therefore be less than in the quadrat.

The plot apparatus used consisted of two steel rods linked by a chain 2.26m long. One end of each rod was sharpened to a point. One rod, driven into the ground, was used as an axis to which the freely swivelling chain was attached. The second rod, attached to the other end of the chain, was used to scribe a circumference on the ground. Care was taken that the rods were kept in a vertical or almost vertical position to the ground. The rods were made of mild steel, one metre long and one centimetre in diameter. The chain, made of chromed metal links, was attached to the rods by brass swivels.

The grasses in the plot were examined by moving the scribe for a convenient distance along the plot perimeter to produce a segment of a circle; a small segment being used when grasses were dense. The grasses in the segment were recorded from the perimeter towards the centre of the plot so that unexamined portions were trampled as little as possible as recording proceeded.

It was decided that 350 plots distributed over the Reserve would be sufficient for obtaining a sample of the

grass communities. It was also decided to take a stratified sample of the grass communities by allocating 315 of the plots to areas occupied by the nine woody communities resulting from the normal analysis of woody plants; and by allocating the remainder of 35 plots to areas of Grassland.

The 315 plots were allocated in the following way. Seven landscape units were selected from each of the woodland communities; the landscape units selected being the first seven listed by the computer print-out for the community. Five plots were distributed in each of the seven landscape units.

The remainder of 35 plots were allocated to seven landscape units having a Grassland vegetation: five plots were distributed in each of the seven landscape units.

The five plots in each landscape unit, whether having a Woodland or a Grassland vegetation, were distributed along a traverse at 50 pace intervals. The traverse was started at any convenient point in the landscape unit, and was aligned more or less parallel to the length of the landscape unit as seen on an airphoto.

One field sheet used for each plot included a record of the following information: the grass species present; the mean height of the bulk of the grasses, but not including exceptionally tall or short plants if these were few in number; the names of the most abundant grasses - these being regarded as the dominants; and visual estimates of percentage grass cover and of percentage forb cover. Cover was estimated on the basis of Greig-Smith's definition (1964, p 5) "as the proportion of ground occupied by perpendicular projection on to it of the aerial parts of individuals of the species under consideration".

Grazing pressure was crudely estimated by a consideration of the general conditions in the plot, including the extent to which grass defoliation was evident, and the proportion of the plot not covered by grass. A numerical value for grazing pressure was awarded on the basis of: no or only slight grazing pressure equivalent to zero, light grazing pressure equivalent to one, moderate to two, heavy to three, and very heavy to four. A typical, slightly grazed plot would show only a few grass leaves grazed, a grass cover of about 50 percent and more, and only a few forbs present. A

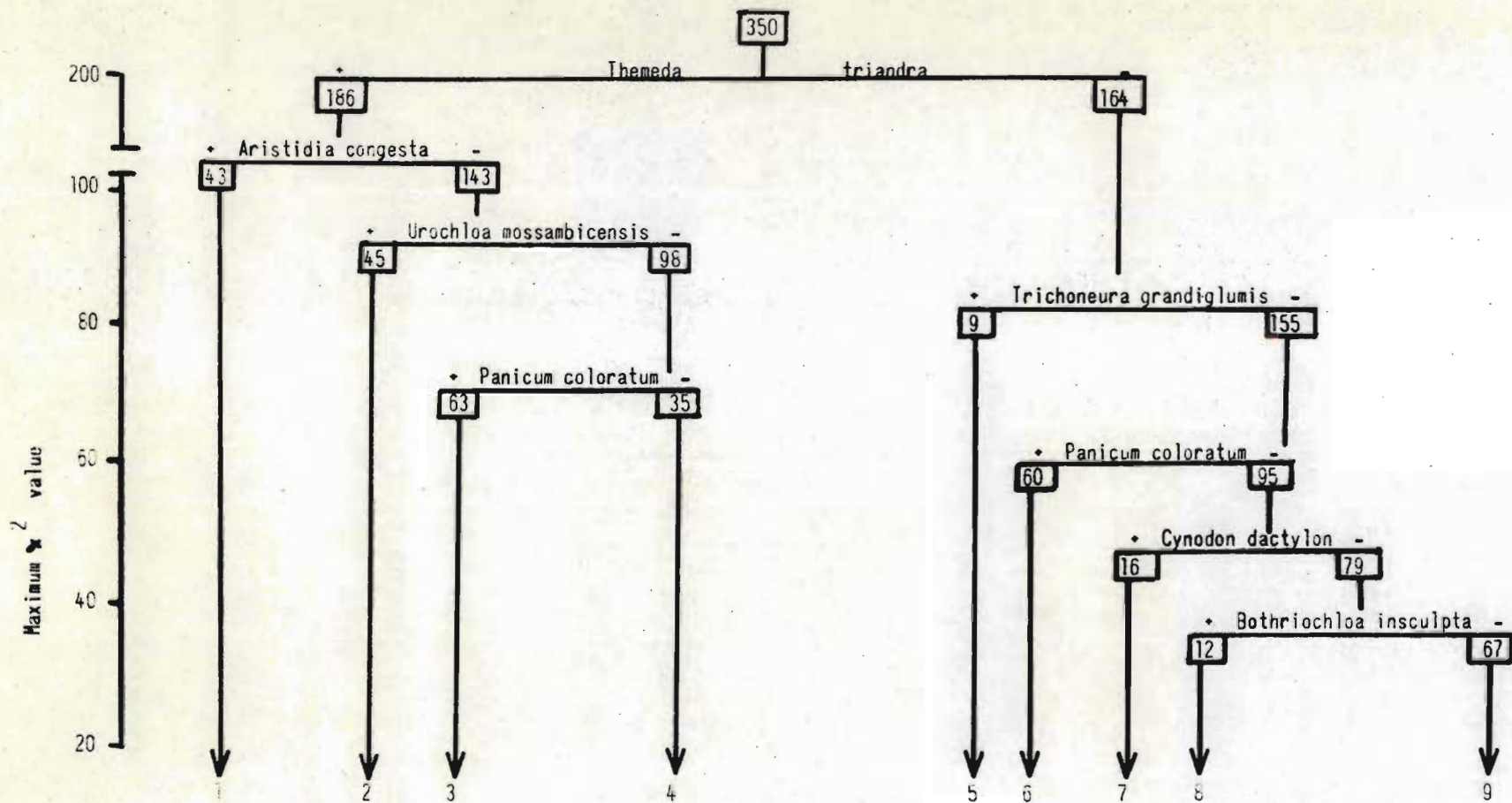


Fig. 4. Classification of 350 grass plots into nine groups by normal analysis.

very heavily grazed plot would contain closely-cropped grasses, a grass cover of 10 percent and less, and many forbs.

Sampling was done during March, 1969, which was at about the time of peak grass growth towards the end of the summer growing season. The measurements of grass height and the estimates of percentage grass cover are, therefore, greater than would be found at most other times of the year; either during the dormant winter when herbage removed by grazing is not replenished by new growth, or during the earlier part of summer when the grasses are still growing and have not yet attained maximum development. Many of the grasses recorded during sampling had to be identified on vegetative characters, even though most grass species were flowering in March, because their inflorescences had been removed by grazing.

3.4.3. Analysis and results

The presence -and-absence records for each of the plots were transferred to punch cards and computed for normal analysis as described for the trees and shrubs (Chapter 3.3.3.).

The normal analysis resulted in a hierarchical classification of the sample population, consisting of 350 plots, into 16 groups of plots at long division level. The classification was, however, intelligible at a short division level represented by the nine groups of plots as shown in Fig.4.

INSERT FIG. 4

The results of the normal analysis were taken into the field for evaluation when the following main features were noticed.

The nine groups corresponded with the main grass communities present in the Reserve. The definitive species responsible for segregation of a group in Fig. 4 were the dominant or co-dominant species of the communities. The grass communities were, therefore, named according to the definitive species of the relevant groups as shown in Fig.4, and given in Table 9. For example, Group 1 in Fig. 4 is given as the Themeda-Aristida Community in Table 9. Group 9 is not given a definitive species in Fig. 4, but is named the Panicum maximum

Table 9. Summary of some characteristics of nine grass communities in Umfolozi Game Reserve. Group numbers taken from Figure 4.

Group	Community	Mean grass height cm	Mean grass cover %	Mean forb cover %	Mean grazing pressure %
1	Themeda-Aristida	40	18	9	35
2	Themeda-Urochloa	45	27	7	45
3	Themeda-Panicum	59	39	3	30
4	Themeda	78	59	2	13
5	Trichoneura	84	28	4	18
6	Panicum coloratum	24	16	25	80
7	Cynodon	59	21	11	55
8	Bothriochloa	60	34	18	32
9	Panicum maximum	50	10	30	47

Community, this being the most abundant and tallest growing species found in the plots constituting Group 9.

The five plots taken from within the same landscape unit were sometimes classified into the same group, but were more often classified into two, three or more, groups. More than one grass community was therefore usually present in a landscape unit; and any one stand of a Woodland community often contained more than one grass community. But six of the nine communities were consistently distributed over predominantly clay soils, and hence will be called the Claysoil Grass Communities; and the other three, consistently distributed over predominantly sandy soils, will collectively be called the Sandsoil Grass Communities.

The original 350 field sheets, representing the 350 plots, were sorted into the nine communities corresponding with the groups to which they had been allocated by the normal analysis. Information from the field sheets on grass height, grass cover, forb cover, and grazing pressure, was abstracted. Mean values for these criteria were calculated for each community and are summarised in Table 9. The mean grazing pressure values in Table 9 are shown as percentages.

INSERT TABLE 9

Species percentage constancy values for each community were calculated as was done for the woody plants. The values are presented in Tables 11 to 19 when the relevant grass communities are described (Chapter 4.2.1.). Species having constancies of ten percent and less are omitted from the Tables because their contribution to the communities was insignificant.

3.4.4. Chemical content

The following experiment was done towards investigating the chemical composition of grasses growing on illuviated clay soils of the Bottomland Association, on eluviated clay soils of the Upland Association, and on sandy soils. Three grasses, Panicum deustum, P. maximum and Themeda triandra were selected for experimentation. Samples of each species were cut from three localities on eluviated clay soils

Table 10. Nutrient content analysis of 24 samples of Panicum deustum, P.maximum and Themedia triandra taken from localities on eluviated, illuviated and sandy soils in Umfolozi Game Reserve during November, 1969.

SOIL	Panicum deustum % of dry weight								Panicum maximum % of dry weight								Themedia triandra % of dry weight							
	n	Prot	P	Ca	Mg	K	Na	N	n	Prot	P	Ca	Mg	K	Na	N	n	Prot	P	Ca	Mg	K	Na	N
ELUVIATED	1	7.57	.103	.14	.19	0.79	.32	1.21	2	8.25	.117	.20	.34	1.12	.32	1.32	3	4.33	.042	.07	.10	.40	.03	0.69
	4	8.34	.099	.09	.25	0.88	.26	1.33	5	8.95	.104	.19	.31	1.06	.26	1.43	6	4.95	.058	.12	.12	.52	.05	0.79
	7	7.41	.139	.14	.21	0.83	.24	1.19	8	11.71	.172	.11	.29	1.14	.34	1.87	9	4.20	.060	.10	.11	.40	.02	0.67
	Total:	23.32	.341	.37	.65	2.50	.82	3.73	28.91	.393	.50	.94	3.32	.92	4.62	13.48	.160	.29	.33	1.32	.10	2.15		
	Mean:	7.77	.114	.12	.22	.83	.27	1.24	9.64	.131	.17	.31	1.11	.31	1.54	4.39	.053	.10	.11	.44	.03	.72		
ILLUVIATED	10	12.41	.133	.14	.26	1.02	.44	1.99	11	16.96	.162	.13	.51	1.37	.37	2.71	12	7.92	.131	.07	.18	0.92	.05	1.27
	13	14.00	.293	.09	.27	0.99	.42	2.24	14	14.16	.127	.11	.41	1.13	.40	2.27	15	8.69	.114	.06	.18	0.87	.07	1.39
	16	11.35	.154	.09	.23	1.12	.34	1.82	17	13.48	.148	.15	.40	1.25	.30	2.16	18	6.74	.105	.04	.13	0.80	.03	1.08
	Total:	37.76	.580	.32	.76	3.13	1.20	6.05	44.60	.437	.39	1.32	3.75	1.07	7.14	23.35	.350	.17	.49	2.59	.15	3.74		
	Mean:	12.59	.193	.11	.25	1.04	0.40	2.02	14.87	.146	.13	.44	1.25	.36	2.38	7.78	.117	.06	.16	0.86	.05	1.25		
SANDY	19	19.72	.150	.16	.35	1.16	.36	3.16	20	10.83	.160	.11	.34	1.16	.25	1.73	21	5.94	.062	.03	.11	0.63	.06	0.95
	22	12.15	.202	.07	.30	1.25	.35	1.94	23	12.62	.155	.08	.33	1.23	.28	2.02	24	5.89	.079	.06	.14	0.60	.06	0.94
	Total:	31.87	.353	.23	.65	2.41	.71	5.10	23.45	.315	.19	.67	2.39	.53	3.75	11.83	.141	.09	.25	1.23	.12	1.89		
	Mean:	15.94	.176	.12	.33	1.25	.36	2.55	11.73	.158	.10	.34	1.20	.27	1.88	5.92	.075	.05	.13	0.62	.06	.95		

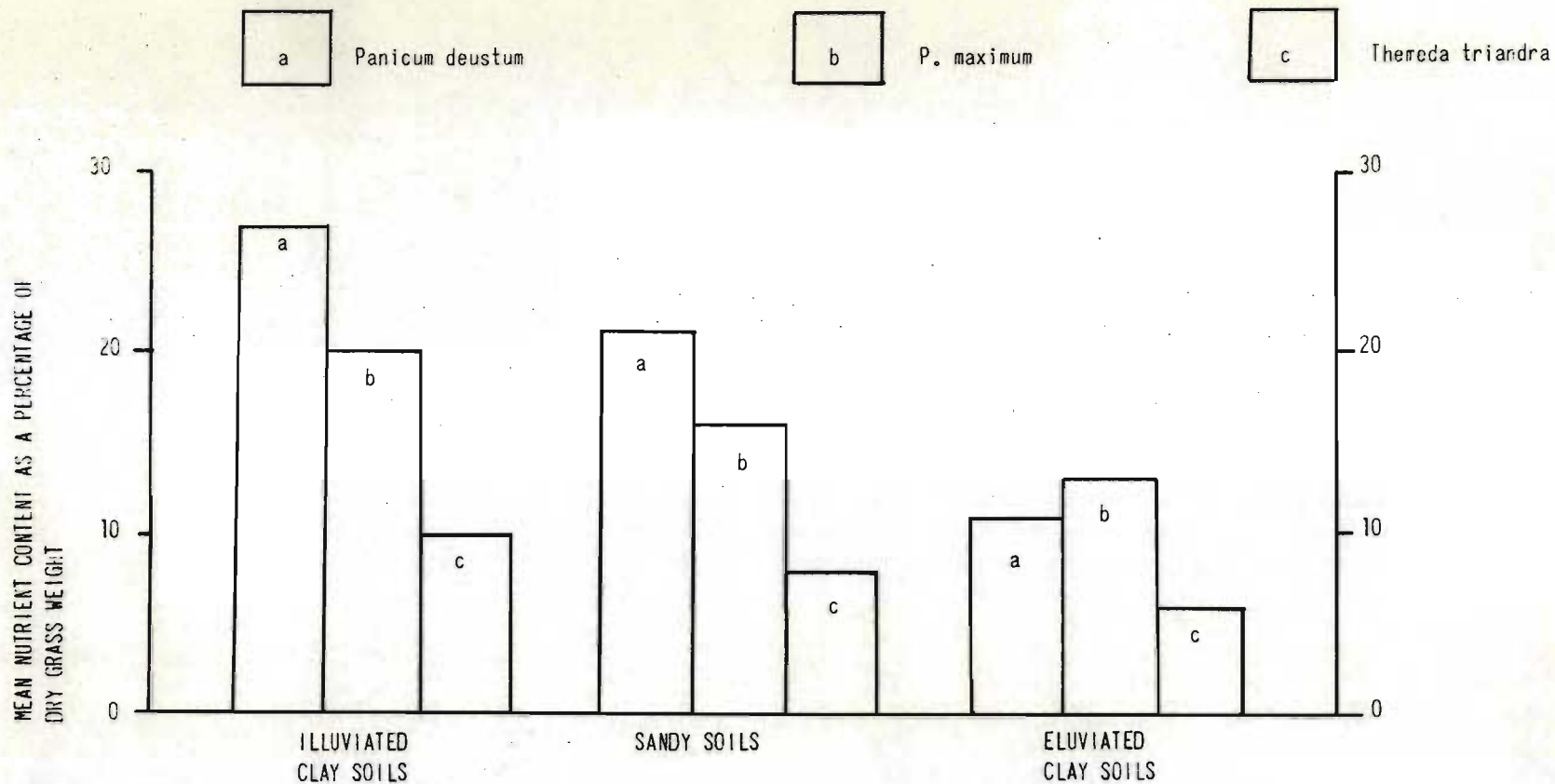


Fig. 5. Histogram showing the mean analysed nutrient content (Protein, P, Ca, Mg, K, Na, N) as a percentage of the dry weights of Panicum deustum, P. maximum and Themeda triandra sampled on three different soil situations.

(the Miocene Surface at Mpila, at Mpila encane, and at Khukho); from three illuviated clay localities (the Quaternary Surface at Mbhuzane, at Thobothi and at Sontuli); and from two localities on sandy soil (the Pliocene Surface at Madlozi, and the Quaternary Surface at Gqoyini). A total of 24 samples was thus obtained during the third week of November, 1969. Sufficient fresh grass material was cut for each sample to almost fill an unused new, plastic bag of 50 kg capacity.

The grass samples were sun-dried, sealed in plastic bags and sent to Cedara College for oven drying and analysis for protein, P, Ca, Mg, K, Na, and N nutrient content. The results of analysis are detailed in Table 10 and are summarised in histogram, Fig. 5.

INSERT TABLE 10 and FIG. 5

Two main features are seen in the results of the chemical analysis. Firstly, that the highest nutrient content is contained by the grasses taken from the carbonate-rich illuviated clay soils; that the grasses taken from the sandy soils have an intermediate nutrient content; and that the grasses taken from the eluviated clay soils have the lowest nutrient content, which is about one half of the amount of nutrients held by the grasses from illuviated clay soils. Secondly, that different amounts of nutrients are contained by the three grasses taken from any one locality. Panicum deustum generally contained the highest amounts of nutrient, except on the eluviated clay situation where it held slightly less than P. maximum, followed by P. maximum, and Themeda triandra contained the lowest amount of nutrient.

The three grasses seem, therefore, to reflect in their nutrient contents the fertility of the soils where they grow. Other grasses, apart from the three species tested, may well also behave so in the Reserve. Grasses in Natal generally do reflect local soil fertility (Mr R. Ludorf, pers. com.).

CHAPTER FOUR

THE PLANT ECOLOGY

4.1. The plant successions

4.1.1. Introduction

A general idea of the plant successions is obtainable from Fig. 6. The successions start with pioneer communities in water, on sand, dry ground or on rock. The pioneer communities pass in most areas into a Themeda triandra var. trachyspatha dominated Grassland which is maintained by frequent fires and which forms part of the climax pattern of Grassland and Woodland. However, where the grasses are not burned sufficiently often, or where there is protection from fire, the Grassland is invaded by woody plants and a Woodland vegetation develops.

INSERT FIG.6

4.1.2. Priseres

4.1.2.1. Hydrosere

Hydroseral communities are poorly represented in the Reserve because of the limited extent of perennial water, and because of unstable conditions in the aquatic habitats. The swift summer floods of the rivers would flush away any unattached aquatic plants. Churning of the unstable, sandy river beds during floods, as well as an abrasive action of the heavy sediment load suspended by the flooding rivers, eliminates all but the most strongly rooted and tough aquatic plants. Few aquatic plants survive in the seasonal pools of standing water contained by the smaller pans away from the rivers, and in the few perennial springs. The smaller pans and the springs are used as wallows by rhinoceros and other animals. Apart from direct damage caused to water plants by the animals, the water is kept so turbid that sufficient light for plant growth can hardly penetrate the surface of the pools.

Delicate aquatic plants characteristic of early hydroseral stages are, therefore, most likely to be found in

the perennial, stagnant water of the large Mgqizweni Pan (Photo 15) which, at depths of two metres and more, is mostly too deep to permit wallowing by animals. The Pan was not investigated because of the several crocodiles which can always be seen on the banks, or partly immersed in the slightly murky water, provided the Pan is approached quietly. However, some of the following early aquatic plants noted in fairly similar pans elsewhere in Zululand, at Lake Sibayi and in the Pongola System, may well also be present in Mgqizweni Pan. The aquatic plants include unattached species of Pistia, of Lemna, and of Azolla; and some attached species of Potamogeton, of Nymphaea, of Lagarosiphon, and of Nitella.

Several aquatic species were found, but in small numbers, in the smaller pans (Photo 13) during rainy seasons when the pans contained water for several weeks. Free-floating plants of Utricularia inflexa were found in the pans even though their waters were very muddy. Two annual sedges, Cyperus difformis and Cyperus sp. (collection no. 688), were present on the pan perimeters but mostly in places where protected by overhanging tree boughs from wallowing animals. An aquatic fern, Marsilea macrocarpa, plants of Alternanthera sessilis and of Echinochloa colonum were found on the pan perimeters; these three species have tough rooting systems and were able to survive in spite of trampling and wallowing.

The first aquatics to appear in shallow pools on river banks include occasional plants of Juncus oxycarpus, Cyperus fastigiatus, Scirpus spp. and seedlings of Phragmites spp. The most extensive hydrosereal communities are reedbeds of Phragmites mauritianus and P. australis that stabilise parts of the banks of the larger pans (Photo 15) and the rivers (Photo 27). The extensive, strong rhizomes and the tough, fibrous nature of the reeds enables them to establish in the loose, easily transported sands, and to withstand the force and abrasive action of floods to the extent that islands of reedbeds have colonised sand in the middle of the river and the stream beds, as in parts of the White Umfolozi River (Photo 4), of the Fuyeni (Photo 12) and Munywane (Photos 19, 22) Streams. The reeds are rarely totally immersed, except by the deepest floods, because of their tall height of three metres. The reeds are, therefore, well adapted to withstand the considerable

fluctuations in water depth, from zero to two metres and rarely more, experienced in the streams and rivers.

The reedbeds are succeeded by a zone of shorter, about one metre high, coarse, stoloniferous grasses. The stoloniferous grasses grow in areas which are inundated for several days during and after floods. Such places include the low-lying ground on the perimeters of the larger pans, a narrow zone situated further up the river banks beyond the reedbeds, and parts of some stream beds, notably near the confluence of the Fuyeni Stream with the White Umfolozi River where the stoloniferous grasses form an extensive Grassland (Photo 12). The Grassland consists of a dense matted growth dominated by Panicum meyerianum; other common grasses include Hemarthria altissima, Paspalum commersonii, Ischaemum arcuatum, Echinochloa crus-galli, Imperata cylindrica and Sorghum halepense.

4.1.2.2. Psammosere

Stages of the psammosere occur on areas of sandy alluvia of the Riverine Soil Association (Chapter 2.4.3.) that are drier than the areas occupied by the hydrosere communities.

A first stage of the psammosere is on recent accumulations of sand deposited by floods. The sand dries out soon after the flood waters have receded. The sand is colonised by pioneer grasses, mostly annuals, including Tragus berteronianus, Chloris pycnothrix, C. virgata, Eleusine indica, Perotis patens, Dactyloctenium giganteum and Rhyncheletrum villosum. These annual grasses are, however, short lived and are susceptible to damage caused through trampling and churning of the loose, sandy substrate by the many animals which move over these parts in search of water. The annual grasses are, therefore, few in number and are soon succeeded by a more vigorous, lawn-like growth of perennial, stoloniferous grasses better adapted to withstand the trampling. Cynodon dactylon is the dominant; other stoloniferous grasses present are Urochloa mossambicensis, Digitaria longiflora and Paspalum distichum.

4.1.2.3. Lithosere

Communities of the lithosere are distributed over



Photo 29. Many shrubs and a few trees have become established on this fragmented scarp to form small patches of Thicket. Some pioneer species persist, namely, Euphorbia tirucalli (left centre) and Ficus sp. (lower right). A few baboons are on the uppermost rock ledge next to a projecting tree of Ficus sp. Mhlolokazana, 27.3.70.



Photo 30. A dense Thicket grows on the south-east aspect, steeply inclined, bouldery, debris slope. A Themeda triandra dominated ground layer, shown in the foreground, is part of an Open Woodland which extends over less steep terrain from the Thicket margin towards the hill top. Mpila Camp is visible on the horizon. Mpila, 11.5.70.

rocky parts of the Reserve, including scarps and some debris slopes, where fire is mostly precluded.

The first colonisers of rock are several kinds of crustose lichens, but these were not collected for identification purposes. More important pioneer plants which establish their roots in the cracks and fissures of vertical rock faces include mostly succulent species and some figs (Photo 28). The succulents include bushes of Euphorbia tirucalli, often the dominant, and Portulacaria afra, short rosette plants of Aloe vanbalenii, and the trailing vines of Cissus quadrangularis. The figs, including Ficus soldanella, F. cordata, F. ingens, F. pretoriae, F. stuhlmanii and F. petersii, can send their roots for long distances, even 20m, down the rock faces. In some instances, as on the Quaternary scarps at Mhlolokazana and Mphafa (Photo 28), the fig roots reach seasonal pools of water in rivers or streams situated at the foot of the scarps.

INSERT PHOTOS 28, 29

The next lithoseral stage is seen where parts of the scarp faces are fragmented and less steep as a result of weathering, as at Mhlolokazana (Photo 29). Plant roots, particularly of the Ficus spp., assist in weathering by forcing rock crevices wider apart. Small patches of fairly dense Thicket, as shown in Photo 29, develop in the widened crevices and in spaces amongst the tumbled rocks which form a bouldery scree at the foot of the fragmented scarp. The Thicket patches, about three metres high, are formed by a profusion of shrubs and some trees. The succulent Euphorbia tirucalli, which is present along with the other succulents, can dominate in places but an obvious dominant is not usually discernible amongst the many other species: Diospyros glandulifera, D. dichrophylla, Garcinia livingstonei, Dombeya cymosa, Combretum erythrophyllum, Terminalia phanerophlebia, Erythrina humeana, Thespesia acutiloba, Ehretia rigida, Xeromphus rudis, Nuxia oppositifolia, Dichrostachys cinerea, Tarchonanthus camphoratus, Brachylaena ilicifolia, Grewia caffra, G. monticola, Plectroniella armata, Cassine aethiopica, Canthium spinosum,



Photo 31. Gaps in the tree and shrub strata of the Combretum apiculatum Closed Woodland allow some light to reach the ground layer. A large tree of Spirostachys africana (left), a shrub of Maytenus senegalensis (right), and large grass tufts of Panicum deustum (near the tree base and at the lower right corner) grow in pockets of soil between the boulders. Fire cannot easily burn through the discontinuous ground layer interspersed by the boulders. The tree and the shrub have retained foliage in the dry season. North aspect scarplet near Mphafa Stream, 10.5.70.

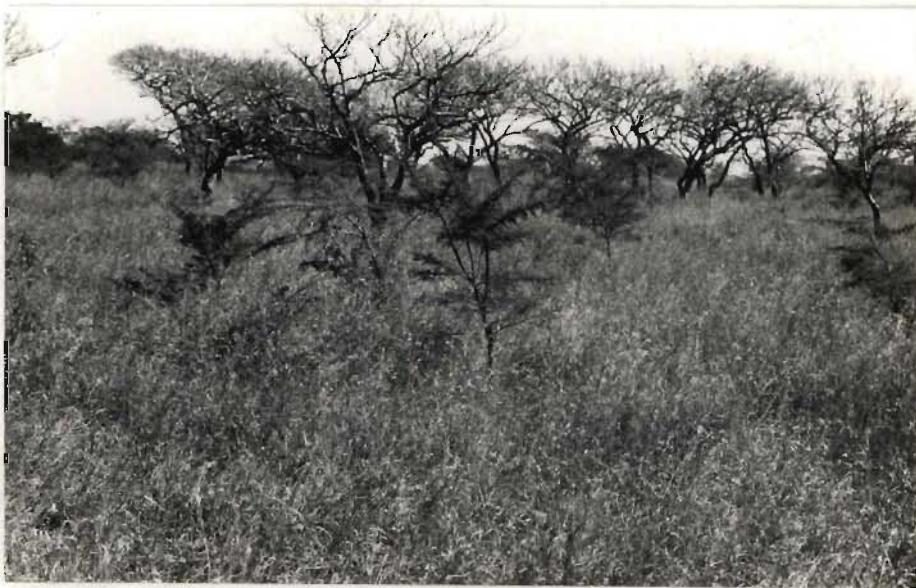


Photo 32. A lightly grazed stand of the Themeda Community has died back in winter to leave a dense litter of tinder dry straw. The litter has not been burned for at least three years, and the small, fire-intolerant saplings of Acacia gerrardii and A. nilotica have consequently outgrown the grasses. Note that the Acacia spp. saplings have not yet shed their leaves, whilst the unusually dense stand of Sclerocarya caffra trees (background) is leafless. Miocene Surface at Ishenilentombi, 6.7.70.

Strychnos spp., Dinocanthium hystrix, Erythroxylon emarginatum, E. delagoense, Vangueria infausta, Pouzolzia hypoleuca, Phyllanthus reticulatis, Kraussia floribunda, Croton menyhartii, Euclea natalensis, Jasminum multipartitum, Turraea floribunda, and more. A few trees which emerge above the Thicket patches include Schotia brachypetala, Commiphora harveyi, Pseudocassine transvaalensis, Combretum apiculatum, and some of the figs listed earlier. Some climbing and scrambling species include Rhoicissus tomentosa, Tecomaria capensis, Strophanthus gerrardii, Entada wahlenbergii, and Dioscoris spp.

More extensive and denser stands of Thicket develop on the comparatively moist, south-east aspect, rocky debris slopes as at Ngabaneni and Mpila (Photo 30). These denser stands of Thicket are fairly similar in composition to the patchy stands on the fragmented scarps, but are so dense that the short, succulent species are shaded out. The substrate, consisting of boulders separated by shallow pockets of dark, highly organic and immature soil, is partly covered by a litter of undecomposed leaves. The substrate is heavily shaded for the greater extent but there is a sparse ground layer consisting of a few shade tolerant plants. The dominant is a sedge Schoenoxiphium lehmanni. The ground layer becomes denser where occasional openings in the Thicket canopy permit additional light to reach the ground, and where some grasses of Panicum deustum, P. maximum and Diplachne eleusine grow. The ground layer is nevertheless too sparse to permit the passage of fire.

INSERT PHOTOS 30, 31

A late stage of the lithosere is represented on the scarplets of terraced topography where a fringe of Combretum apiculatum Closed Woodland grows along the scarplets (Photo 18). The Closed Woodland comprises three strata. The uppermost stratum, about seven metres high, is dominated by Combretum apiculatum; other important trees include Spirostachys africana, Acacia burkei, Schotia brachypetala and Pappea capensis. The middle stratum, about three metres high, is of fairly dense shrubs and small trees similar in composition to the dense

Thicket described earlier. Rather more light reaches the ground in the Closed Woodland than in the Thicket because of frequent gaps in the tree and shrub strata (Photo 31). The ground layer is, therefore, better developed than in the Thicket and comprises large tufts of Panicum deustum and P. maximum. Many species of forbs, of which Strelitzia regina is the most conspicuous, are also present. The ground layer is confined to pockets of soil lying between boulders, and is so discontinuous that fires, which easily burn through adjacent areas of Open Woodland on the benches, rarely penetrate the Closed Woodland (Photo 31). But in some less rocky, better grassed places the incursions of fire thin out the Closed Woodland and a Combretum apiculatum Open Woodland results, as shown in Figure 6. The Open Woodland arises, however, most often as the result of woody plants invading areas of Grassland as described in Chapter 4.1.3.2.

Not yet mentioned in this description of the lithosere are horizontal, or almost horizontal, rock ledges. Some rock ledges are found on scarps where a rock fragment has broken away, and others are where a rock ledge outcrops above the soil surface. Pioneer plants of the grass Rhyncheletrum repens lodge in cracks on the rock ledges. A detritus of rock grit and gravel accumulates in shallow depressions on the rock ledges. The detritus is colonised by a few small and a few larger plants. The small plants include some succulents, Crassula sp., Portulaca quadrifida and P. kermesina; two grasses, Tragus berteronianus and Tripogon minimus; as well as four sedges, Cyperus rupestris, C. teneriffae, Kyllinga erecta and Bulbostylis boeckeleriana. The larger plants are grasses including Rhyncheletrum repens, which is the dominant, Sporobolus nitens, S. stapfianus and Chloris virgata. These grasses represent an initial stage of the grass successions to be described in the next section.

4.1.3. Later stages

4.1.3.1. Grass successions

4.1.3.1.1. Introduction

Early and later grass successions, falling

outside the priseres of water, sand and rock, are found in dry localities where stratified soils have developed or are in the process of maturation. The early stages commence with the invasion by short grasses of bare areas and gradually pass, through the replacement of short grasses by taller grasses, into the later stages.

Although the successional development of grass communities on sandy and clay soils is similar in most respects, some differences in species composition between the communities require that they be treated separately.

4.1.3.1.2. On sandy soil

The earliest grasses to colonise areas of bare sand, mostly found on the Springfield Series overlying sandstone (Chapter 2.4.1.) are small, mostly less than 20cm tall, annual species including the following: Tragus berteronianus, Rhyncheletrum repens, R. villosum, Chloris pycnothrix, Perotis patens, Eragrostis cilianensis, E. gummiflua, Tricholaena monachne, Trichoneura grandiglumis, Sporobolus pyramidalis, Stipagrostis stipitata and Eleusine indica. Perennial Cynodon dactylon can also be present and, where so, is often the dominant.

A large number of mostly perennial, mid-seral grasses soon establish at a high density amongst the short annuals so that the latter are shaded out. The mid-seral grasses grow from 20 to 40 cm high and include the following species amongst others: Eragrostis capensis, E. ciliaris, Aristida congesta, Heteropogon contortus, Urochloa mossambicensis, Digitaria argyrograpta, D. polevansii, Panicum coloratum and Pogonarthria squarrosa.

The latest stage is apparent when tall, from about 50 to 100 cm, climax grasses overtake the mid-seral grasses. Themeda triandra is the dominant, other tall grasses include Panicum maximum, Digitaria macroglossa, Cymbopogon plurinodis, Eustachys paspaloides, Sporobolus fimbriatus and Hyperthelia dissoluta.

4.1.3.1.3. On clay soil

The earliest grass to colonise areas of bare,

clay soil is Tragus berteronianus which grows to about 10 cm tall. These other short, up to about 20 cm high, mostly annual species also invade bare areas in more or less the following sequence: Chloris pycnothrix, Sporobolus smutsii, S. nitens and Digitaria argyrograpta, a perennial.

The preceding pioneer stage is succeeded by a mid-seral stage of perennials dominated by about 40 cm tall Urochloa mossambicensis. Other common mid-seral grasses include Panicum coloratum, Digitaria polevansii, Eragrostis capensis and Heteropogon contortus.

The climax stage is brought about when Themeda triandra invades and dominates the community at a height of about 80 cm. Other typical, less abundant although often emergent species of the climax stage include Panicum maximum, Digitaria macroglossa, Setaria woodii, Eustachys paspaloides, Cymbopogon validus and Diheteropogon amplexans.

4.1.3.1.4. Seasonal aspects

4.1.3.1.4.1. Grasses

Since winter temperatures are not sufficiently low to be limiting factors for plant growth in the Reserve, the grasses recover from winter dormancy soon after moisture is supplied by the first rains of summer.

Recovery of the grasses is shown by the production and elongation of new green shoots. The grasses flower later on at about the time when shoot elongation ceases. Although many of the species do not seem to flower in any particular month of summer, some flower early and others late. The following grasses, mostly annuals, are conspicuous amongst the early flowering species: Bothriochloa inculpta, Tragus berteronianus, Eragrostis spp., Sporobolus spp., Chloris virgata, and Brachiaria serrata. Late flowering species include Themeda triandra, Panicum spp., Digitaria spp., Aristida congesta, Diplachne eleusine, Rhyncheltrum repens, Trachypogon spicatus, Elyonurus argenteus and Cymbopogon spp.

A very marked seasonal succession of grasses, whereby a series of even taller and later flowering grasses overtopped shorter and earlier flowering grasses, is reported by Downing (1966) for a Grassland at Tabamhlope, near Estcourt

(Fig.1). The Tabamhlope Grassland experiences a reliable summer rainfall, and is in an area from which grazing animals were largely precluded. Although some of the grasses at Tabamhlope are also represented in the Reserve, no such conspicuous seasonal succession of grasses was noted. Seasonal succession in the Reserve is apparently obscured by the erratic and unreliable nature of the summer rains; late rains, or spells of drought during the growing season, delay or retard grass development. The amount of growth and the times of flowering of the grasses in the Reserve vary somewhat from year to year. Seasonal succession is also obscured because many inflorescences are removed by heavy grazing.

INSERT PHOTO 32

The aerial portions of the grasses die back from the leaf and culm tips as the dry season sets in, and the leaves persist during winter as a tinder-dry straw consisting largely of fibre and cellulose (Photo 32). Weinmann (1955, pp 580-582) and Nursey (1971, pp 157-159) have demonstrated that die back, during times of drought, in Southern African grasses is accompanied by a translocation, from the leaves to the roots, of some of the starch, protein and mineral content. Losses in the protein and acid-soluble ash contents of 48 and 40 percent respectively are reported for herbage at the end of the growing season by Weinmann (1955, p 583). Grasses in the Reserve are, therefore, probably of much less food value to herbivores during winter than in summer; and considerably lower levels of nutrient contents, than are shown in Table 10 for summer, are expected for winter. A low protein content, to the order of two percent, is indicated by Weinmann (1955, p 580) for some grasses in winter.

Humification of the tinder-dry straw in the Reserve, as would likely happen in a more humid climate, is negligible or very slow because of the arid winter and because the straw likely contains insufficient nutrients for a vigorous microbial population. The straw accumulates, therefore, as a highly inflammable litter. Litter sufficient for burning accumulates after one season's growth in areas of dense grass which are lightly or moderately grazed.

4.1.3.1.4.2. Associated forbs

Many forbs associated with the grasses enter at early stages of the grass successions. The associated forbs are divisible into two groups. The one group is associated with areas of dense, less heavily grazed grasses mostly found on soils of the Upland Association. The other group is found in areas of sparse, heavily grazed grasses found on soils of the Bottomland Association.

The upland forbs are short growing, mostly less than 15 cm high, and include the following species amongst others: Commelina benghalensis, Thunbergia dregeana, T. atriplicifolia, Ruellia patula, Polygala serpentaria, Vigna longiloba, Chascanum schlecteri, and on sandy soils, Aster luteus, A. muricatus and Stylosanthus fruticosa. These forbs correspond with the class of vernal aspect plants described by Bayer (1955, pp 546-547). The short, vernal aspect plants are able to compete against the tall, 50 to 100 cm, grasses by flowering and setting their leaves early in the season, usually by December, before being overgrown by the grasses. Some vernal aspect plants in the Reserve, including Scilla spp., Ammocharis falcata, Anthericum galpinii and Aneilema sinicum, store moisture in swollen underground organs over the winter. Such plants are thus able to set flowers and leaves even before the first rains of summer because they contain moisture and food reserves stored over from the previous summer.

Forbs are more numerous on soils of the Bottomland Association and, in the most heavily grazed places, outnumber the grasses. The forbs range from short, less than 30 cm to tall, about 50 cm and more, plants. The short plants include Aizoon glinoides, Blepharis integrifolia, Tribulus terrestris, Heliotropium steudneri, Cyphocarpa angustifolia, Abutilon sp., Lasiosiphon splendens, Crossandra fruticosa, Orthosiphon australis, Phyllanthus maderaspatensis, Gomphrena celosoides and Aptenia cordifolia. The tall plants include Asparagus virgata, Asparagus spp., Ekbolium amplexicaule, Cienfuegosia hildebrandtii, Nidorella residifolia, Helichrysum undatum, Justicia flava, Lycium sp., Hibiscus pusillus and Gossypium transvaalense.

Most of the bottomland forbs flower later in the season, usually after December, and correspond with the

class of autumnal aspect plants described by Bayer (1955, pp 547-548). Some of the forbs seem, however, to flower at any time during summer and, in the case of some annuals like Aizoon glinoides, more than one generation might be produced in the course of a summer.

The shorter forbs on bottomlands areas are successful partly because competition from taller grasses is much reduced, or even eliminated, through heavy grazing. The taller forbs are sufficiently high to compete with any tall grasses for light but are easily broken off by trampling and are less numerous than the shorter forbs of Aizoon glinoides and Blepharis integrifolia which are less sensitive to trampling, and which are sometimes the dominants of the ground layer in bottomlands.

4.1.3.1.5. The role of fire

Fire plays an important ecological role in the Reserve mainly through incinerating the litter of straw which remains in the dry season after the grasses and forbs have died back. A periodic burning off of the litter, usually done at some time in August or September, seems essential for promoting a vigorous regrowth of new grass shoots in the summer following the winter dormancy. In areas which are left unburned for lengthy periods of about five or more years, the accumulated litter from several seasons' growth becomes so dense as to over-shade the grass bases. New, short grass shoots stimulated by the rains of summer do not grow successfully in the heavy shade; the grass tufts, particularly of climax stage species like Themeda triandra, eventually become moribund at their centres.

Removal of the litter by fire is also of importance to the short, vernal aspect forbs. Bayer (1955, pp 546-547) describes how the forbs are suppressed and eventually eliminated through over-shading if the litter is not removed.

On the other hand, frequent burnings of the litter at one, two or three year intervals suppress, retard or eliminate the growth of young woody plants including seedlings and saplings.

The climax, Themeda triandra dominated stage of the grass successions is thus maintained in areas which are burned sufficiently often. The Themeda triandra Grassland is invaded by woody plants in areas which are not burned sufficiently often, or which are heavily grazed, so that



Photo 33. This area was kept clear of woody plants during the period from 1932 to 1952. The dense stand of spindly Acacia karroo trees, all about the same height, may have established at about the same time during the period between 1952 and 1956, when the use of fire was discouraged in the Reserve. The trees, although not yet fully mature, are tall and less easily damaged by fire than the short saplings shown in Photo 32. Notice, however, that the dead, lowermost branches on some of the trees are within the reach of grass fire flames. The dense, dry litter of the Themeda Community has not recently burned, and a younger generation of A. karroo seedlings invades the grasses. Miocene Surface of Khukho, 7.5.70.



Photo 34. A bare termite mound where grasses do not grow. Many grass culms and leaves around the mound have been removed by termites and herbivores. Madlozi, 9.5.70.

Woodland replaces the Grassland, as shown in Fig. 6.

Shade intolerant Themeda triandra is replaced, where the ground layer is shaded by woody invaders, by grasses more tolerant of shade: Panicum deustum, P. maximum, Enteropogon monostachyos and Diplachne eleusine. If the shaded areas are also heavily grazed, then Dactyloctenium australe is often abundant.

4.1.3.2. Invasion by trees, shrubs and climbers

Mature trees and shrubs in the Reserve are fire tolerant and are rarely killed by fire. Their trunks and branches are protected from fire by a thick, insulating bark. The bark in many species is ridged, as in most Acacia spp., or flakey as in Sclerocarya caffra and Spirostachys africana. Less well protected parts, including leaves and finer stems, escape fire damage where tall crowns stand a few metres beyond the reach of flames (Photo 33). Some young and older woody plants can respond to fire damage by coppice regrowth from their bases near soil level. Notable coppice producing species include Acacia caffra, A. tortilis and Euclea spp.

INSERT PHOTO 33

But young woody plants, including seedlings and saplings up to about five years old (Photo 32) are much less resistant to fires. The rather delicate crowns and thin-barked stems of such plants are at about the same height, or slightly taller, as the grasses and, being within the reach of flames, are easily charred by a passing blaze (Photo 32). Successful establishment of the woody plants depends, therefore, on the degree of protection from fires during the early stages of growth.

Rocky scarps and scarplets, as at Mhlolokazana (Photos 6, 29) and Chibilenyathi (Photos 17, 18), are fire-free or very rarely burned. Plants growing in the soil pockets of scarplets and debris slopes are sheltered from fire by the intervening boulders (Photo 31). Protection from fire in these habitats permits the successful development of the dense woody communities characteristic of the Lithosere, whether of Thicket (Photo 30) or of Combretum apiculatum Closed Woodland

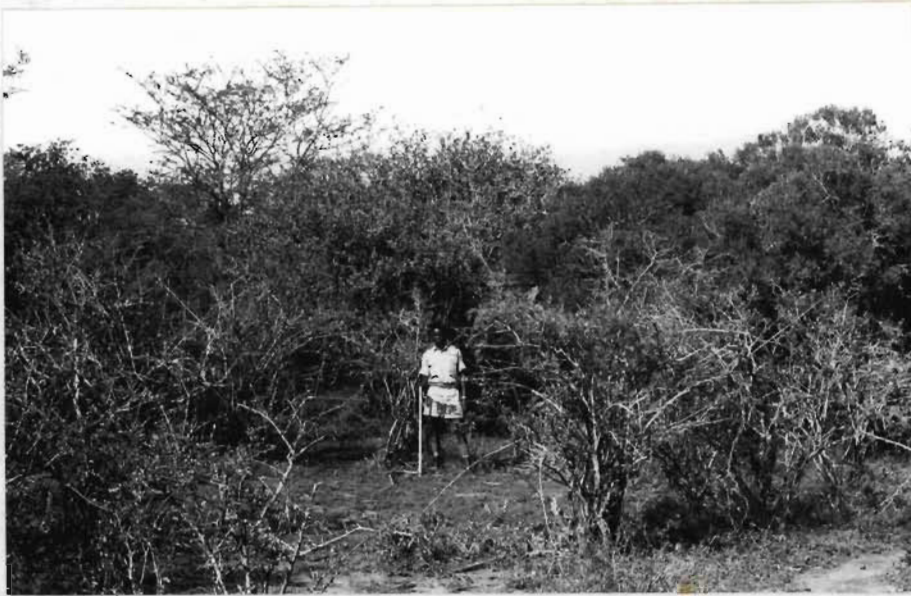


Photo 35. A Thicket of Brachylaena illicifolia (foreground), of Maytenus senegalensis (background, centre), and of dense Euclea undulata (background, right). A tree of Acacia grandicornuta rises above the Thicket. Fires cannot burn through the sparse, overgrazed Panicum maximum Community in the foreground. Quaternary Surface at Mfulamkhulu, 10.5.70.

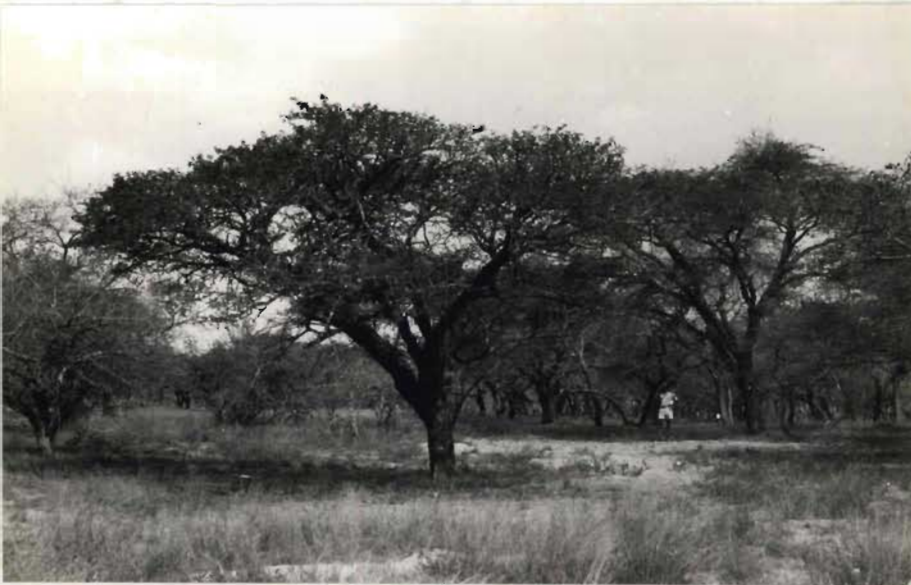


Photo 36. An interrupted ground cover of the 40cm tall Themeda - Aristida Community reveals white patches of the loose, sandy Springfield Soil. The grasses form the lowermost stratum of Acacia burkei Woodland. The small, pale tree to the left is Zizyphus mucronata; the large trees with wide crowns are A. burkei. Gqoyini, 8.5.70.

(Photo 18)

INSERT PHOTO 34

Some protection from fire is provided on termite mounds (Photo 34). Plants, apart from some fungi, do not grow on the mounds whilst they are inhabited by termites. The termites also maintain a fire-free zone around a mound by removing the dead aerial portions of grass during winter. When the mound is burrowed out and broken up by an antbear and is subsequently abandoned by the termites, grasses and woody plants invade the mound. Fire-free conditions are, however, maintained on the mound because herbivores, particularly white rhinoceros and wildebeest, are especially fond of the grasses there and keep them grazed short. The woody plants, at first including shrubs of Maytenus senegalensis, Schotia capitata and Thespesia acutiloba, and later including trees of Cussonia zuluensis, Spirostachys africana and Pseudocassia transvaalensis amongst others, can thus develop to maturity and form the Bush Clumps of Mixed Woodland (Photo 26).

INSERT PHOTO 35

The absence of fire in the heavily grazed bottomlands has promoted a widespread development of Thickets over many parts of the Quaternary Surface. The Thickets occur either in small patches, a few metres in diameter and separated by intervals of about ten metres, or as extensive stands occupying a hectare and more. Mature stands attain heights of between three and five metres. Some stands formed by Acacia luederitzii are so dense that they are impenetrable by man (Photo 25). Other common Thicket constituents are Euclea spp., Maytenus senegalensis, Brachylaena ilicifolia and Tarchonanthus camphoratus (Photo 35).

The tree and shrub invaders of Grassland provide support for climbing and scrambling plants which appear early in the woody succession. The climbers and scramblers include Asparagus spp., Capparis tomentosa, Cissus rotundifolia, C. quadrangularis, Sarcostemma sp. and, on Riverine soils, Acacia brevispica.

Table 11. Percentage constancy values of grasses in the Cynodon Community. Results based on a group of 16 plots.

Climax	<i>Panicum maximum</i>	100
Mid-seral	<i>Urochloa mossambicensis</i>	48
Early	<i>Cynodon dactylon</i>	100
	<i>Dactyloctenium giganteum</i>	42
	<i>Tragus berteronianus</i>	24
	<i>Sporobolus pyramidalis</i>	18
	<i>Eragrostis</i> spp.	12
	<i>Rhyncheletrum villosum</i>	12

The invasion of the ground layer terminates in three different Woodland Associations, as shown in Fig. 6, according to the soil association present. Acacia-Combretum Open Woodland is the climax on soils of the Upland Association, Acacia-Spirostachys Closed Woodland is the climax on the Bottomland Association, and Acacia-Ficus Riverine Woodland is the climax on soils of the Riverine Association.

4.2. The Main Communities

4.2.1. Grass Communities

4.2.1.1. Sandsoil Communities

4.2.1.1.1. The Cynodon Community

The Cynodon Community is the most extensive grass community on the Riverine Soil Association where it forms a lawn-like ground cover (Photo 27).

INSERT TABLE 11

The Community composition, given in Table 11, shows a preponderance of those species typical of early stages in the grass successions. Perennial Cynodon dactylon, at a constancy of 100 percent, is the dominant in open and less heavily shaded parts; other early grasses in the open parts include annual species of Dactyloctenium giganteum (42 percent), Tragus berteronianus (24 percent), Sporobolus pyramidalis (18 percent), Eragrostis spp. (12 percent), and Rhyncheletrum villosum (12 percent). Only one mid-seral grass, Urochloa mossambicensis (48 percent), and one climax grass, Panicum maximum (100 percent) are present.

The P. maximum succeeds C. dactylon in shaded places where the grasses have been invaded by woody plants. The high, 100 percent constancy of P. maximum is a reflection of the considerable extent of invasion by the woody plants. Panicum maximum also grows in the open but at a much lower density than in the shade. The woody plants have invaded because the grasses, at a mean height of 59 cm and with a cover of 34 percent, are not sufficiently competitive. The mean

Table 12. Percentage constancy values of grasses in the Themeda-Aristida Community. Results based on a group of 43 samples.

Climax	<i>Themeda triandra</i>	100
	<i>Eustachys paspaloides</i>	49
	<i>P. maximum</i>	39
	<i>Digitaria macroglossa</i>	30
	<i>Sporobolus fimbriatus</i>	14
	<i>Bothriochloa insculpta</i>	14
	<i>Cymbopogon plurinodis</i>	14
Mid-seral	<i>Aristida congesta</i>	100
	<i>Eragrostis capensis</i>	70
	<i>Panicum coloratum</i>	58
	<i>Heteropogon contortus</i>	54
	<i>D. polevansii</i>	27
	<i>Urochloa mossambicensis</i>	25
	<i>Digitaria argyrograpta</i>	14
Early	<i>Tragus berteronianus</i>	50
	<i>Eragrostis</i> spp.	25
	<i>Sporobolus pyramidalis</i>	23
	<i>Tricholaena monachne</i>	20
	<i>Eragrostis cilianensis</i>	16
	<i>Rhyncheletrum repens</i>	16
	<i>Trichoneura grandiglumis</i>	14

height of 59 cm combines values for grasses which are protected from grazing by the woody invaders, and which can grow to one or two metres high in the case of P. maximum, together with values for unprotected grasses which are kept short, at a few centimetres, by grazing. A moderate grazing pressure of 55 percent is recorded for the Community as a whole. Forb cover is low at 11 percent.

4.2.1.1.2. The Themeda-Aristida Community

The Themeda-Aristida Community is the characteristic ground layer over sandy, loose soils of the Springfield Series in Acacia burkei Woodland. The Community has a moderate height of 40 cm and a sparse cover of 18 percent even though only lightly grazed at a pressure of 35 percent. Sand bathing, mostly by white rhinoceros, is largely responsible for many bare patches of soil not occupied by the Community (Photo 36). No fires were seen in the Community during the course of this study although the grass patches would burn easily if they were individually ignited.

/INSERT PHOTO 36 and TABLE 12/

The many species, listed in Table 12, composing the Community are widely representative of climax, mid-seral and early stages in the succession. Notable climax grasses are Themeda triandra, a co-dominant at a constancy of 100 percent, Eustachys paspaloides (49 percent), Panicum maximum (39 percent) and Digitaria macroglossa (30 percent). Commoner mid-seral grasses include the other co-dominant, Aristida congesta (100 percent), Eragrostis capensis (70 percent), Panicum coloratum (58 percent) and Heteropogon contortus (54 percent). The early stage grasses are less common except for Tragus berteronianus (50 percent).

Some of the more palatable, climax grasses of T. triandra, E. paspaloides, P. maximum and D. macroglossa are evidently being replaced by some much less palatable, mid-seral grasses of A. congesta and E. capensis as a result of selective grazing. Although grazing pressure at 35 percent is from light to moderate for the Community as a whole, animals show a strong preference for the more palatable species and avoid the others.

Table 13. Percentage constancy values of grasses in the Trichoneura Community. Results based on a group of nine plots.

	<i>Panicum maximum</i>	66
Climax	<i>Sporobolus fimbriatus</i>	33
	<i>Hyperthelia dissoluta</i>	33
	<i>Eragrostis capensis</i>	38
	<i>Aristida congesta</i>	66
Mid-seral	<i>Heteropogon contortus</i>	55
	<i>Pogonarthria squarrosa</i>	55
	<i>Urochloa mossambicensis</i>	33
	<i>Trichoneura grandiglumis</i>	100
	<i>Sporobolus pyramidalis</i>	55
Early	<i>Tragus berteronianus</i>	44
	<i>Tricholaena monachne</i>	44
	<i>Digitaria polevansii</i>	44
	<i>Rhyncheletrum repens</i>	33

Competition from the more palatable climax grasses is consequently reduced and the less palatable, mid-seral grasses proliferate. Aristida congesta has taken over as the single dominant in places where T. triandra has been grazed out, as in an abandoned horse paddock at Mhlolokazana Outpost.

The high incidence of the early stage T. berteronianus is ascribed to trampling and sand bathing by animals. These activities on the loose sand appear to discourage forb growth which is low at nine percent even though the sparse grass cover is not highly competitive.

4.2.1.1.3. The Trichoneura Community

The Trichoneura Community is of limited occurrence in the Reserve: only nine out of the 350 grass plots were allocated by the classification to this Community. All nine of the plots are situated on sandy soil close to some old kraal sites on Khukho.

INSERT TABLE 13

The composition of the Community, given in Table 13, shows that climax stage grasses are outweighed by mid-seral and early grasses. Only three climax species are represented, Panicum maximum, Sporobolus fimbriatus and Hyperthelia dissoluta; Themeda triandra is notably absent. Mid-seral species are well represented by Eragrostis capensis, Aristida congesta, Heteropogon contortus and Pogonarthria squarrosa. Early stage grasses predominate through the presence of Trichoneura grandiglumis, Sporobolus pyramidalis, Tragus berteronianus, Tricholaena monachae, Digitaria polevansii and Rhyncheletrum villosum. There is no obvious dominant in the Community which has been named after T. grandiglumis which is the most constant species present although it is shorter than 20 cm.

The absence of T. triandra and the large proportion of mid-seral and early grasses, notably T. grandiglumis, is ascribed to past human habitation when the land might have been heavily grazed or cultivated. The tall, 84 cm height of the Community is due to the presence of the tall climax species, including Hyperthelia dissoluta which is a favourite thatching grass currently harvested in winter from

Table 14. Percentage constancy values of grasses in the Bothriochloa Community. Results based on a group of twelve plots.

Climax	Bothriochloa insculpta	100
	Panicum maximum	64
	P. deustum	16
	Cymbopogon plurinodis	16
	Diplachne eleusine	16
Mid-seral	Aristida congesta	88
	Eragrostis capensis	16
Early	Sporobolus nitens	56
	Chloris pycnothrix	32
	S. smutsii	32
	Tragus berteronianus	32
	Eragrostis spp.	24
	Eragrostis cilianensis	16

the Khukho area. The climax grasses are not so dense as to preclude the growth of the shorter mid-seral and early grasses. Overall grass cover is 28 percent, but forb cover is very low at four percent.

4.2.1.2. Claysoil Communities

4.2.1.2.1. The Bothriochloa Community

The Bothriochloa Community is mostly distributed on soils of the Bottomland Association either as a ruderal community in recently dug road drains (Photo 10), or in isolated patches, usually much less than one hectare in extent, surrounded by larger areas of heavily grazed grasses. The Community is tall, at 60 cm, has a fairly good grass cover of 34 percent, but has a high proportion of forbs at a cover of 30 percent.

INSERT TABLE 14

The Community composition, given in Table 14, shows a high proportion of the early stage grasses which are pioneers of bare soil, such as Sporobolus nitens at a constancy of 56 percent, Chloris pycnothrix (32 percent), S. smutsii (32 percent), Tragus berteronianus (32 percent), Eragrostis cilianensis (16 percent) and other Eragrostis spp. (24 percent). Mid-seral grasses are not conspicuous apart from Aristida congesta (88 percent). Climax grasses are conspicuous; two of them including the dominant Bothriochloa inculpta (100 percent) and Cymbopogon plurinodis (16 percent) grow in the open, but the others including Panicum maximum (64 percent), P. deustum (16 percent) and Diplachne eleusine (16 percent) are mostly found in the shelter of trees and shrubs which have invaded the Community.

The early stage grasses, which are highly palatable, are being replaced through selective grazing in the bottomlands by later grasses, particularly by less palatable plants of A. congesta, B. inculpta and C. plurinodis. The latter two species are highly aromatic and are probably amongst the least palatable of grasses in the Reserve. The other, more palatable climax grasses in the Community, P. maximum, P. deustum

Table 15. Percentage constancy values of grasses in the Panicum maximum Community. Results based on a group of 67 plots.

Climax	Panicum maximum	84
	P. deustum	40
	Enteropogon monostachyos	27
	Diplachne eleusine	21
Mid-seral	Urochloa mossambicensis	42
Early	Tragus berteronianus	52
	Sporobolus smutsii	21
	Dactyloctenium australe	11

and D. eleusine, survive beneath the crowns of many woody plants where they are protected from grazing. A moderate grazing pressure of 32 percent for the Community as a whole incorporates values for the more heavily and for the less heavily grazed species.

Although B. insculpta behaves as a climax species in areas of undisturbed soil, it is also a pioneer of recently disturbed soil in road drains.

Fires rarely reach the isolated patches of the Community as the surrounding areas are usually too sparse for the passage of fire.

4.2.1.2.2. The Panicum maximum Community

The Panicum maximum Community is common in heavily grazed bottomlands and sometimes surrounds patches of the Bothriochloa Community. The P. maximum Community is so heavily grazed, at a pressure of 47 percent, that it has the sparsest grass cover, at 10 percent, of all grass communities in the Reserve (Photos 14, 37) and cannot be burned. The lack of grass competition and the absence of fires have permitted a very dense growth of forbs, at a cover of 30 percent, and an invasion by many shrubs and small trees.

INSERT PHOTO 37, TABLE 15

Table 15 shows that few species constitute the Community. The early stage grasses, Tragus berteronianus at 52 percent constancy and Sporobolus smutsii (21 percent), and one mid-seral grass, Urochloa mossambicensis (42 percent), form a very sparse, short cover in open areas accessible to grazing between the woody invaders. The climax grasses, including the dominant Panicum maximum (84 percent), P. deustum (40 percent), Enteropogon monostachyos (27 percent) and Diplachne eleusine (21 percent), are all particularly palatable and are mostly found in the shelter from grazing provided by the woody invaders and where they can attain heights of over one metre. Panicum maximum also grows in the open but is kept grazed to within a few centimetres of the ground. The other three climax grasses, as well as the early stage



Photo 37. An eight metre tall stand of Acacia grandicornuta Closed Woodland includes a shorter, dark leaved tree of Pappea capensis (left). The overgrazed, short, Panicum maximum grass Community is too sparse for burning, and is invaded by woody plants, including a sapling of A. grandicornuta (lower margin, left) and a multi-stemmed shrub of Maytenus senegalensis (right). Quaternary Surface at Sontuli, 7.5.70.



Photo 38. The square lips of the white rhinoceros enable it to crop the grasses to within a few centimetres of the ground. Persistent over-grazing brings about the short and sparse conditions of the Panicum coloratum Community which is insufficiently dense for burning. Trees of Acacia tortilis and A. nilotica are behind the animals; branches of Zizyphus mucronata and A. nigrescens appear on the left and right margins respectively. Pliocene pediment near Tobothi, 23.10.69.

Table 16. Percentage constancy values of grasses in the Panicum coloratum Community. Results based on a group of sixty plots.

Climax	Panicum maximum	50
	Bothriochloa insculpta	18
	Cymbopogon plurinodis	13
	Diplachne eleusine	12
Mid-seral	Panicum coloratum	100
	Urochloa mossambicensis	75
	Eragrostis capensis	15
Early	Sporobolus smutsii	48
	S. nitens	46
	Tragus berteronianus	41
	Digitaria argyrograpta	27
	Eragrostis spp.	25

Dactyloctenium australe (11 percent), prefer shade.

4.2.1.2.3. The Panicum coloratum Community

The Panicum coloratum Community is also found on bottomlands but, unlike the P. maximum Community, also extends over some pediments. The P. coloratum Community is the most heavily grazed, at a pressure of 80 percent, in the Reserve and is the favourite grazing of the white rhinoceros. Heavy grazing keeps the grasses short, at 24 cm, and maintains a low grass cover of 16 percent (Photos 3, 38). Although forb cover is high at 25 percent, it seems that the overgrazing of the Community and the absence of fire are comparatively recent because few young tree and shrub invaders are present compared with the P. maximum Community.

INSERT PHOTO 38, TABLE 16

The composition of the P. coloratum Community, given in Table 16, shows that early and mid-seral grasses outweigh climax species. The early species include Sporobolus smutsii, at a constancy of 48 percent, and Tragus berteronianus (41 percent), both of which are present but to a lesser degree in the Panicum maximum Community (Table 15), as well as S. nitens (46 percent), Digitaria argyrograpta (27 percent) and Eragrostis spp. (25 percent) which are not represented in the P. maximum Community. The dominant is a mid-seral grass P. coloratum (100 percent) which is absent from the P. maximum Community; another conspicuous mid-seral grass is Urochloa mossambicensis (75 percent) which is better represented here than in the P. maximum Community. The only conspicuous climax species is P. maximum (50 percent) which is here more poorly represented than in the P. maximum Community.

The higher proportion and dominance of mid-seral grasses indicates that the P. coloratum Community is successionaly more advanced than the P. maximum Community. The climax species are, however, less well represented in the P. coloratum Community where there are fewer tree and shrub invaders for protection from grazing than are found in the P. maximum Community. The lower number of the woody invaders in the P. coloratum Community is also shown by the absence of P.

deustum, Dactyloctenium australe and Enteropogon monostachyos, and by lesser amounts of P. maximum and Diplachne eleusine, all of which are shade loving species.

The two mid-seral grasses, P. coloratum and U. mossambicensis, are amongst the favourite food grasses of the white rhinoceros. The two grasses are so successful because they are well adapted to withstand, to some considerable extent, the heavy and persistent grazing. Because the two grasses have a stoloniferous and prostrate habit, a fair proportion of their foliage lies so close^{to} the ground as to escape defoliation when grazed. Retention of some foliage at each grazing permits regrowth. The same applies to the early stage grasses which lose only a portion, perhaps as much as one third, of their foliage at each grazing because they are short growing, and because their leaves are mostly held very close to the ground, often in the form of a rosette (T. berteronianus, Sporobolus nitens, S. smutsii) or of a tight bunch (D. argyrograpta). On the other hand, the tall growing climax species can lose 90 percent or more foliage at each grazing; repeated grazing so reduces vigour that the climax grasses die out. The highly palatable climax grasses, including the P. maximum, P. deustum, Diplachne eleusine and Enteropogon monostachyos, are thus more successful in the P. maximum Community, where there is better protection afforded by woody plants from grazing, than in the P. coloratum Community which has fewer woody invaders. The unpalatable climax species of Bothriochloa insculpta and Cymbopogon plurinodis present in the P. coloratum Community do not require protection by woody plants from grazing for their survival.

4.2.1.2.4. The Themeda-Urochloa Community

The Themeda-Urochloa Community (Photo 39) is common on pediments and ridges of the Pliocene Surface and occurs on soils of both the Bottomland and the Upland Association. The Community is much less grazed, at a pressure of 45 percent, than the Panicum coloratum Community (80 percent), and is consequently much taller at 45 cm (24 cm) and denser with a grass cover of 27 percent (16 percent). Because of greater competition from the grasses, forb cover is much lower at seven percent in the Themeda-Urochloa Community than in the P.



Photo 39. The short Themeda - Urochloa Community surrounds isolated patches of the taller Themeda - Panicum Community. The short grasses are too sparse for burning; the tall grass patches burn readily if individually ignited. Short growing, broad leaved, geophytic plants of Ammocharis falcata succeed in the short grass areas where grass competition is reduced by grazing; A. falcata is absent from the tall grass patches which are very rarely burned off. Pediments of the Pliocene Surface at Madlozi, 24.10.69.



Photo 40. A bush-clumped, Acacia nilotica Mixed Woodland grows on a gently sloping pediment of the Pliocene Surface. A lone bush of Euclea shimperi on the right is sufficiently mature to withstand fires that have periodically burned the dense, extensive stand of the Themeda - Panicum Community. The Miocene summit of Sokwezele lies on the skyline near the centre of the photo, and Zintunzini rises on the left. Madlozi, 23.10.69.

Table 17. Percentage constancy values of grasses in the Themeda-Urochloa Community. Results based on a group of 45 plots.

Climax	Themeda triandra	100
	Panicum maximum	50
	Cymbopogon plurinodis	35
	Bothriochloa insculpta	35
	Digitaria macroglossa	22
Mid-seral	Urochloa mossambicensis	100
	P. coloratum	86
	D. polevansii	28
	E. capensis	26
Early	Digitaria argyrograpta	39
	Sporobolus smutsii	26
	Eragrostis spp.	26
	Tragus berteronianus	22
	S. nitens	17

coloratum Community (25 percent). The Themeda-Urochloa Community is nevertheless mostly too sparse for the passage of fire (Photo 39).

INSERT PHOTO 39, TABLE 17

The composition of the Community, given in Table 17, shows a considerably higher presence of climax and mid-seral grasses than of early grasses. The climax grasses include Themeda triandra, a co-dominant at a constancy of 100 percent, Panicum maximum (50 percent), Cymbopogon plurinodis (35 percent), Bothriochloa insculpta (35 percent) and Digitaria macroglossa (22 percent). The mid-seral grasses include the other co-dominant, Urochloa mossambicensis (100 percent), Panicum coloratum (86 percent), Digitaria polevansii (28 percent) and Eragrostis capensis (26 percent). The early grasses include Digitaria argyrograpta (39 percent), Sporobolus smutsii (26 percent), Eragrostis spp. (26 percent), Tragus berteronianus (22 percent) and S. nitens (17 percent).

The Community contains more climax and mid-seral grasses than the Panicum coloratum Community (Table 16) and is, therefore, successionally more advanced. Notable differences between the two Communities include a first appearance of climax grasses of T. triandra and D. macroglossa, and of mid-seral D. polevansii, in the Themeda-Urochloa Community. The same early grasses occur in both Communities, but their presence is lower in the Themeda-Urochloa Community because of greater competition from the taller mid-seral and climax grasses.

Woody invaders are even less numerous than in the P. coloratum Community and, because the extent of shaded areas is lower, the shade loving Diplachne cleusine is not present in the Themeda -Urochloa Community.

4.2.1.2.5. The Themeda-Panicum Community

The Themeda-Panicum Community is mostly distributed on soils of the Upland Association on hilltops of the Miocene Surface (Photo 20), but is also common on ridges and pediments of the Pliocene Surface where it either occurs in small patches associated with the Themeda-Urochloa

Table 18. Percentage constancy values of grasses in the Themeda-Panicum Community. Results based on a group of 63 plots.

Climax	Themeda triandra	100
	Digitaria macroglossa	45
	Panicum deustum	37
	P. maximum	35
	Cymbopogon plurinodis	33
	Eustachys paspaloides	28
	Bothriochloa insculpta	17
Mid-seral	Panicum coloratum	100
	Eragrostis capensis	29
	Heteropogon contortus	22
	D. polevansii	11
Early	D. argyrograpta	25
	Tragus berteronianus	17
	Eragrostis spp.	15

Community (Photo 39), or covers more extensive areas (Photo 40). The Themeda-Panicum Community is less heavily grazed, at a pressure of 30 percent, than the Themeda-Urochloa Community (45 percent) and is somewhat taller at 59 cm (45 cm) and denser with a grass cover of 39 percent (27 percent). Woody invaders are few in number because the extensive areas of the Community are fairly regularly burned and because, in both the extensive and patchy areas, competition from the dense grass cover discourages establishment of the woody seedlings as well as of forbs, which have a very low cover of three percent.

INSERT PHOTO 40, TABLE 18/

The composition of the Community, given in Table 18, shows that climax species outweigh mid-seral and early species. The climax species include one co-dominant, Themeda triandra at a constancy of 100 percent, Digitaria macroglossa (45 percent), Panicum deustum (37 percent), P. maximum (35 percent), Cymbopogon plurinodis (33 percent), Eustachys paspaloides (28 percent) and Bothriochloa insculpta (17 percent). The mid-seral species include the other co-dominant, Panicum coloratum (100 percent), Eragrostis capensis (29 percent), Heteropogon contortus (22 percent) and Digitaria polevansii (11 percent). Only three early species present are Digitaria argyrograpta (25 percent), Tragus berteronianus (17 percent) and Eragrostis spp. (15 percent).

The Themeda-Panicum Community, which contains more climax and less early grasses, is successional more advanced than the Themeda-Urochloa Community (Table 17). A notable difference between the climax species is the presence in the Themeda-Panicum Community of E. paspaloides, which appears here for the first time, and of shade-loving P. deustum which grows partly shaded by the dense growth of the other, rather taller climax species. Of the mid-seral species, P. coloratum is successful because its weak, otherwise prostrate culms are able to reach light by trailing over the supports provided by the more robust climax plants. Urochloa mossambicensis, which is a co-dominant mid-seral grass of the Themeda-Urochloa Community, is suppressed in the Themeda-Panicum

Table 19. Percentage constancy values of grasses in the Themeda Community. Results based on a group of 35 plots.

	Themeda triandra	100
	Cymbopogon spp.	60
	Panicum deustum	40
	Digitaria macroglossa	40
Climax	Eustachys paspaloides	40
	Diheteropogon amplexans	34
	Setaria woodii	31
	Tristachya hispida	28
	P. maximum	28
	Heteropogon contortus	45
Mid-seral	Eragrostis capensis	20
	Digitaria polevansii	20
	Brachiaria cruciformis	15
Early	Eragrostis spp.	14

Community by competition from the dense growth of the climax grasses. Also suppressed are the early grasses, particularly the Sporobolus spp. which are absent from the Themeda-Panicum Community.

4.2.1.2.6. The Themeda Community

The distribution of the Themeda Community, shown on the vegetation map, is virtually confined to soils of the Upland Association on hill tops of the Miocene Surface (Photos 1, 17, 30). The Community is much less heavily grazed, at a pressure of 13 percent, than the Themeda-Panicum Community (30 percent), and is considerably taller at 78 cm (59 cm) and denser with a grass cover of 59 percent (39 percent). The grass cover is so dense that forb cover is kept very low at two percent. The dense grasses burn fiercely, but in some areas have evidently not been burned very often over the last twenty or so years because woody invaders are fairly numerous (Photos 32, 33).

INSERT TABLE 19

The composition of the Community, given in Table 19, shows that the many climax species are floristically far more important than the few mid-seral and early species. The climax species include the dominant Themeda triandra at a constancy of 100 percent, Cymbopogon spp. (60 percent), Panicum deustum (40 percent), Digitaria macroglossa (40 percent) Eustachys paspaloides (40 percent), Diheteropogon amplexans (34 percent), Setaria woodii (31 percent), Tristachya hispida (28 percent) and Panicum maximum (28 percent). The mid-seral grasses include Heteropogon contortus (45 percent), Eragrostis capensis (20 percent) and Digitaria polevansii (20 percent). The early grasses are Brachiaria eruciformis (15 percent) and Eragrostis spp. (14 percent).

The Themeda Community is successional more advanced than the Themeda-Panicum Community. Climax species of Cymbopogon validus, which is commonest on mesic aspects and which is included with C. plurinodis amongst the Cymbopogon spp. in Table 19, of D. amplexans, S. woodii and of T. hispida,



Photo 41. A dense grass stand of the Themeda Community in the foreground is invaded by woody plants of the Acacia caffra Community. The many low bushes just taller than the grasses are of A. caffra; the tall, dark stemmed trees with large leaves are Dombeya rotundifolia (centre); a tree of A. tortilis (left foreground) stands at the head of a drainage line; the tall, leafless trees are Sclerocarya caffra. Acacia tortilis Open Woodland occupies parts of the lower Pliocene slopes in the middle distance. Further back, the White Umfolozi River flows from right to left below Ndleke scarp. South-east view from the Miocene Surface at Nqolothi, 14.7.69.



Photo 42. A dense stand of the Acacia caffra Community growing on a steep, mesic, south-east aspect. Dombeya rotundifolia (left) retains some large leaves; to its right and beside the figure is a dull grey bush of A. caffra. More trees of D. rotundifolia and the black, gaunt stems of A. karroo are in the middle distance. The dense ground layer is of the Themeda Community. Miocene surface at Mpiła encane, 8.5.70.

appear for the first time in the succession in the Themeda Community. Mid-seral grasses are largely excluded by the dense climax growth and fail to attain co-dominant status with T. triandra; and Panicum coloratum is shaded out. Of the early grasses present in the Themeda-Panicum Community, only the Eragrostis spp. are represented in the Themeda Community which, in addition, contains the early grass B. eruciformis not found elsewhere. The mid-seral and early grasses in the Themeda Community are mostly found where the soil surface is very stony.

4.2.2. Woody Communities

4.2.2.1. The Acacia-Combretum Open Woodland Association

4.2.2.1.1. The Acacia caffra Community

The Acacia caffra Community is mostly found on hilltops of the Miocene Surface and on steep slopes of the Pliocene Surface above 300m altitude. Rare occurrences of the Community below 300m altitude are confined to south aspects. All localities occupied by the Community have shallow and stony soils. Plants of the Community are seen as the early woody invaders of some parts of the Themeda Grassland (Fig.6). The generally small stands, less than five hectares in extent, of the A. caffra Community are so intimately associated with the Themeda Grassland that the distribution of the two Communities could not readily be separated at a scale of 1:50,000; and the two are mapped together on the vegetation map.

INSERT PHOTOS 41,42

Plants of the A. caffra Community are, for the greater part, widely spaced from 20 to 50m apart as shown in Photo 41. But on steeper, mesic, south-east aspects the plants grow more closely spaced by about ten metres and less, as shown in Photo 42. The Community grows to a height of between three and five metres. Tall species of the Community, including Acacia nilotica, A. karroo, A. gerrardii, A. tortilis and Dombeya rotundifolia have a less robust stature when

Table 20. Species percentage constancy (C) and fidelity (S) of plants in the Acacia caffra Community. Results based on a group of 58 samples.

		C	S
Tall species	<i>Acacia nilotica</i>	80	17
	<i>A. karroo</i>	72	33
	<i>A. gerrardii</i>	64	19
	<i>Ziziphus mucronata</i>	52	10
	<i>Dombeya rotundifolia</i>	47	33
	<i>Sclerocarya caffra</i>	45	22
	<i>A. tortilis</i>	31	7
	<i>Combretum apiculatum</i>	22	12
	<i>A. nigrescens</i>	14	4
	<i>Combretum molle</i>	10	30
Short species	<i>A. caffra</i>	88	64
	<i>Ozoroa paniculosa</i>	52	50
	<i>Maytenus heterophylla</i>	52	25
	<i>Rhus pentheri</i>	48	19
	<i>Dichrostachys cinerea</i>	34	9
	<i>Tarchonanthus camphoratus</i>	31	14
	<i>A. senegal</i>	21	11
	<i>Ormocarpum trichocarpum</i>	12	44

SUMMARY

Degree	Percentage range	Quantity of species recorded for each degree of			
		Constancy		Fidelity	
5	80-100	Constantly present	2	Exclusive	0
4	60-79	Mostly present	2	Selective	1
3	40-59	Often present	6	Preferential	2
2	20-39	Seldom	5	Indifferent	5
1	1-19	Rare	3	Strange	10

growing in the A. caffra Community than when in other communities of the Acacia-Combretum Association. Acacia karroo when growing in the A. caffra Community has a peculiar, elongated and spindly growth form (Photo 33) which is rarely seen outside of the Community. Both the spindly and robust forms of A. karroo are mentioned by Ross (1970, p 30), but he does not make any taxonomic separation. Acacia caffra usually grows in the Reserve as a short, less than three metres, multi-stemmed bush resulting from prolific coppice regeneration (Photo 41); robust specimens are rare (Photo 43). Coppice regeneration follows after A. caffra is damaged by fires which occasionally burn through the dense ground layer of grasses. The large, finely divided and feathery leaves are thin and translucent so that A. caffra has an attractive light green appearance in summer, and gives a pale tone on photographic prints.

INSERT TABLE 20

The plants composing the Community are divided into two groups, one of tall and the other of short species, in Table 20 even though stratification is not clearly evident in the field. Of the tall species, Acacia nilotica is constantly present at a constancy of 80 percent; A. karroo (72 percent) and A. gerrardii (64 percent) are mostly present; and often present are Zizyphus mucronata (52 percent), Dombeya rotundifolia (47 percent) and Sclerocarya caffra (45 percent). Seldom present trees are A. tortilis (31 percent) and Combretum apiculatum (22 percent). Acacia nigrescens (14 percent) and C. molle (10 percent) are rare. The short species, almost as numerous as the tall species, include constantly present A. caffra (88 percent); often present Ozora paniculosa (52 percent), Maytenus heterophylla (52 percent) and Rhus pentheri (48 percent); the remaining species listed in Table 20 are of seldom or rare presence.

There are no species of exclusive fidelity to the Community. Acacia caffra, at a fidelity of 64 percent, is the most faithful and only selective species; preferential species are Ozoroa paniculosa (50 percent) and Ormocarpum



Photo 43. Acacia tortilis Open Woodland grows on the distant, south aspect, Pliocene debris slope and on the almost level, Miocene hill top. The leafy crowns of A. tortilis are distinct, but several trees of Sclerocarya caffra have shed their leaves and are inconspicuous. The figure stands beside an unusually robust specimen of A. caffra. A dense grass cover of the Themeda Community extends throughout. Summit of Ngolothi, 14.7.69.

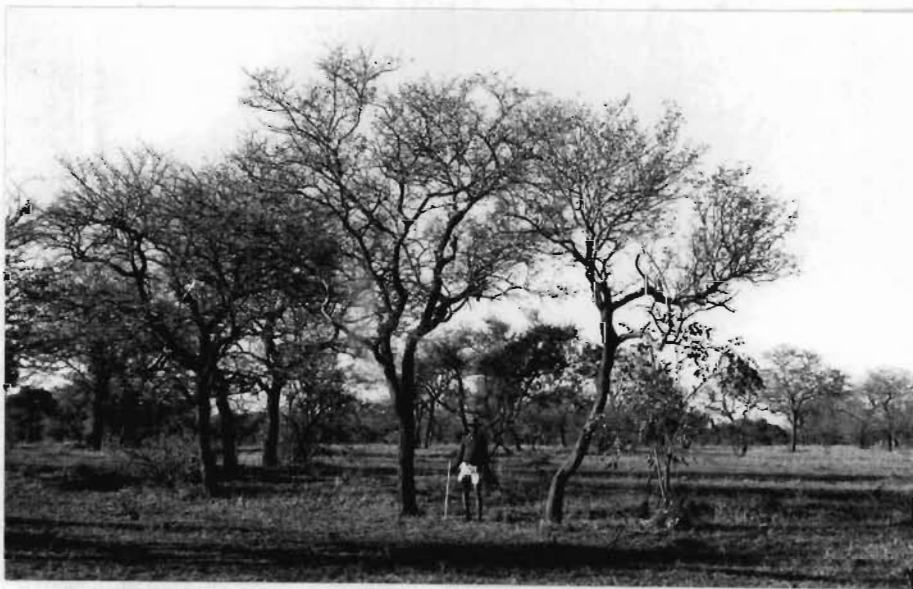


Photo 44. An Open Woodland contains some gnarled, robust trees of Acacia nigrescens with irregularly shaped crowns which retain a few leaves, as well as the graceful shrub Grewia monticola (right) with large leaves. A ground layer of the Themeda - Urochloa Community is grazed short. A gently sloping Pliocene pediment over dolerite at Thobothi, 9.5.70.

Table 21. Species percentage constancy (C) and fidelity (S) of plants in the Acacia tortilis Community. Results based on a group of 58 samples.

		C	S
Tall species	<i>Acacia tortilis</i>	95	22
	<i>Ziziphus mucronata</i>	88	16
	<i>A. nilotica</i>	86	18
	<i>A. gerrardii</i>	72	22
	<i>Sclerocarya caffra</i>	45	22
	<i>A. karroo</i>	35	16
	<i>Boscia albitrunca</i>	26	19
	<i>A. burkei</i>	21	14
	<i>Schotia brachypetala</i>	19	8
	<i>Dombeya rotundifolia</i>	12	8
	<i>Combretum apiculatum</i>	11	5
Short species	<i>Dichrostachys cinerea</i>	38	10
	<i>Rhus pentheri</i>	35	14
	<i>Maytenus heterophylla</i>	24	11
	<i>A. senegal</i>	24	13
	<i>Tarchonanthus camphoratus</i>	21	9
	<i>Euclea daphnoides</i>	19	22
	<i>Brachylaena ilicifolia</i>	15	10
	<i>Gardenia spatulifolia</i>	12	8

SUMMARY

Degree	Percentage range	Quantity of species recorded for each degree of			
		Constancy		Fidelity	
5	80-100	Constantly present	3	Exclusive	0
4	60-79	Mostly present	1	Selective	0
3	40-59	Often present	1	Preferential	0
2	20-39	Seldom	8	Indifferent	4
1	1-19	Rare	6	Strange	15

trichocarpum (44 percent). The other species are of indifferent or strange fidelity.

In some stands of the Community, the short growing A. caffra is dominant but in other stands taller plants of A. nilotica, A. karroo or D. rotundifolia are dominant. The Community is, nevertheless, named after the short growing A. caffra which is the most constant and most faithful constituent. The A. caffra Community could well be seral to the taller A. tortilis Community described in the next section. The tall species in the A. caffra Community are better able to withstand occasional burnings of the dense grass layer and may be increasing more rapidly than the short species, of which A. caffra is the only highly successful representative because it is particularly well adapted to recover by coppicing from fire damage.

4.2.2.1.2. The Acacia tortilis Community

The Acacia tortilis Community grows on shallow, well drained soils on some hills of the Miocene Surface, and on some ridges and pediments of the Pliocene Surface. Examination of the vegetation and topography maps shows that the A. tortilis Community is often distributed in an altitudinal zone immediately below the A. caffra Community, but A. tortilis grows at all altitudes in the Reserve.

INSERT PHOTO 43, TABLE 21

An uppermost stratum of the park-like A. tortilis Community attains a height of about five metres and consists of trees which can be widely spaced, as much as 100m apart as shown in Photos 2 and 24, or more closely spaced from less than about 20m as shown in Photos 20 and 43. A few, widely spaced short species form an indistinct lower stratum which is suppressed by occasional burnings of a dense ground layer, mostly of the Themeda or Themeda-Panicum Communities.

The composition of the A. tortilis Community, given in Table 21, shows a predominance of the tall above the short species, the latter being seldom or rarely present. Constantly present tall species include the flat-crowned

Table 22. Species percentage constancy (C) and fidelity (S) of plants in the Acacia nigrescens Community. Results based on a group of 93 samples.

		C	S
Tall species	<i>Acacia nigrescens</i>	100	52
	<i>Ziziphus mucronata</i>	75	23
	<i>A. tortilis</i>	71	27
	<i>A. nilotica</i>	40	13
	<i>Sclerocarya caffra</i>	34	28
	<i>Combretum apiculatum</i>	32	28
	<i>A. gerrardii</i>	29	14
	<i>Boscia albitrunca</i>	25	30
	<i>Schotia brachypetala</i>	22	15
	<i>Dombeya rotundifolia</i>	18	20
	<i>Ozoroa paniculosa</i>	18	28
	<i>Spirostachys africana</i>	17	8
	<i>Pappea capensis</i>	13	10
	<i>Commiphora spp.</i>	12	48
Short species	<i>Dichrostachys cinerea</i>	50	22
	<i>Maytenus heterophylla</i>	44	33
	<i>Rhus pentheri</i>	40	26
	<i>Tarchonanthus camphoratus</i>	34	24
	<i>Grewia spp.</i>	20	51
	<i>Maytenus senegalensis</i>	18	11
	<i>Acacia senegal</i>	11	9
	<i>Euclea shimperi</i>	10	6

SUMMARY

Degree	Percentage range	Quantity of species recorded for each degree of			
		Constancy		Fidelity	
5	80-100	Constantly present	1	Exclusive	0
4	60-79	Mostly present	2	Selective	0
3	40-59	Often present	4	Preferential	3
2	20-39	Seldom	7	Indifferent	11
1	1-19	Rare	8	Strange	8

dominant A. tortilis (95 percent), Ziziphus mucronata (88 percent), and A. nilotica (86 percent). Acacia gerrardii (72 percent) is mostly present and Sclerocarya caffra (45 percent) is often present. The reasons are not known as to why S. caffra is so abundant in some stands (Photos 20, 32, 43) yet absent from others (Photo 24). The seldom present short species are Dichrostachys cinerea, Rhus pentheri, Maytenus heterophylla and A. senegal.

The Community contains neither exclusive, selective nor preferential species. Four species, A. tortilis, A. gerrardii, S. caffra and Euclea daphnoides are of indifferent fidelity and the other constituents are strange.

4.2.2.1.3. The Acacia nigrescens Community

The Acacia nigrescens Community is very rarely found growing at altitudes above 145m; but at lower altitudes it forms extensive stands, as shown on the vegetation map, that nearly always grow over a dolerite substrate. In only a few localities was it seen growing on rock other than dolerite, as on shale in parts of the Mbuzane and Mbulungu areas. The Kiaora Form soil which develops in situ over dolerite (Chapter 2.4.1.) is the commonest soil under the A. nigrescens Community.

INSERT PHOTO 44, TABLE 22

The Community grows in an attractive Open Woodland (Photo 44) characterised by the irregular, untidy crowns of A. nigrescens. An upper stratum contains robust trees eight metres tall, some of which are widely spaced by about 50m while others are lightly clustered into groups of three or five. A lower stratum contains a number of widely dispersed short species from one to four metres high. A ground layer of grasses is often of the Themeda-Urochloa Community.

The composition of the A. nigrescens Community is given in Table 22. The tall species include the dominant A. nigrescens which is constantly present at 100 percent. Ziziphus mucronata (75 percent) and A. tortilis (71 percent) are

mostly present; A. nilotica (40 percent) is often present; seldom present are Sclerocarya caffra (34 percent), Combretum apiculatum (32 percent), A. gerrardii (29 percent), Boscia albitrunca (25 percent) and Schotia brachypetala (22 percent). The other tall species are rare. The short species are less numerous than the tall; they include often present plants of Dichrostachys cinerea (50 percent), Maytenus heterophylla (44 percent), Rhus pentherii (40 percent) as well as seldom present Tarchonanthus camphoratus (34 percent) and Grewia spp. (20 percent). The Grewia spp. include G. monticola, G. caffra, G. villosus and G. hexamita.

There are no species of exclusive or selective fidelity to the Community. Several preferential species are A. nigrescens (52 percent), Grewia spp. (51 percent) and several Commiphora spp. (48 percent) of which C. neglecta is the commonest. The remaining 29 out of the 32 species recorded for the Community are of indifferent or strange fidelities.

4.2.2.1.4. The Acacia burkei Community

The Acacia burkei Community grows only on sandy soils of the Springfield Series developed over sandstones and quartzites (Chapter 2.4.1.). Extensive stands of the Community, as shown on the vegetation map, are distributed over pediments, but small stands of about one hectare and less are also found where the sandy soil is on benches of the terraced topography. In some places the A. burkei Community forms a mosaic with the Acacia nilotica Community, as along parts of pediments in the Gqoyini catchment, where fragments of an overlying sandstone stratum have weathered away to reveal an underlying shale stratum. The A. nilotica Community grows on the shale. The areas of mosaic A. burkei-A. nilotica are shown on the vegetation map according to which of the two was the most extensive community in the particular landscape unit.

The A. burkei Community grows as a park-like Open Woodland as seen in Photo 36. Magnificent, thick-trunked trees of A. burkei, of average height of seven metres, are often grouped into clusters where their crowns can be in

Table 23. Species percentage constancy (C) and fidelity (S) of plants in the Acacia burkei Community. Results based on a group of 35 samples.

		C	S
Tall species	<i>Acacia burkei</i>	80	33
	<i>Ziziphus mucronata</i>	77	9
	<i>A. nilotica</i>	71	9
	<i>A. gerrardii</i>	51	9
	<i>A. tortilis</i>	43	6
	<i>Combretum apiculatum</i>	34	11
	<i>Sclerocarya caffra</i>	31	10
	<i>A. karroo</i>	23	6
	<i>Peltophorum africanum</i>	23	47
	<i>A. nigrescens</i>	20	4
	<i>Dombeya rotundifolia</i>	20	8
	<i>Schotia brachypetala</i>	20	5
	<i>Pappea capensis</i>	11	3
	<i>Spirostachys africana</i>	11	2
	<i>Terminalia phanerophlebia</i>	11	20
	<i>Sideroxylon inerme</i>	14	6
	<i>Boscia albitrunca</i>	11	5
Short species	<i>Dichrostachys cinerea</i>	74	12
	<i>A. senegal</i>	43	14
	<i>Euclea shimperi</i>	26	6
	<i>Maytenus senegalensis</i>	26	7
	<i>Rhus pentheri</i>	23	6
	<i>Strychnos</i> spp.	20	41
	<i>Canthium spinosa</i>	20	25
	<i>Maytenus heterophylla</i>	20	4
	<i>Gardenia spatulifolia</i>	17	16
	<i>A. caffra</i>	14	6
	<i>E. daphnoides</i>	14	10
	<i>Tarchonanthus camphoratus</i>	14	4
	<i>Grewia monticola</i>	11	8
	<i>Ozoroa paniculosa</i>	11	7

SUMMARY

		Quantity of species recorded in each degree of			
Degree	Percentage range	Constancy		Fidelity	
5	80-100	Constantly present	1	Exclusive	0
4	60-79	Mostly present	3	Selective	0
3	40-59	Often present	3	Preferential	2
2	20-39	Seldom	13	Indifferent	3
1	1-19	Rare	11	Strange	26

contact or spaced 20m apart; but a number of isolated trees grow in open glades, up to 50m wide, that can separate the tree clusters. The spreading, profusely branched crowns have an average diameter of seven metres and more so that the crowns are broader than the trees are high. Irregularly spaced, sometimes densely clumped stands of short species constitute a lower stratum. A patchy ground layer is provided by grasses of the Themeda-Aristida Community (Chapter 4.2.1.1.2).

INSERT TABLE 23

The composition of the A. burkei Community is given in Table 23. The upper stratum contains the dominant A. burkei constantly present at 80 percent, mostly present Ziziphus mucronata (77 percent) and A. nilotica (71 percent), as well as often present A. gerrardii (51 percent) and A. tortilis (43 percent). Of the remaining species in the upper stratum, the more conspicuous include seldom present Combretum apiculatum (34 percent), Sclerocarya caffra (31 percent) and Peltophorum africanum (23 percent). Most short species of the lower stratum are seldom or rare, except for mostly present Dichrostachys cinerea (74 percent) and often present A. senegal (43 percent); but Gardenia spatulifolia (17 percent) deserves mention because of its deeply scented, attractive yellow or white flowers.

The Community contains neither exclusive nor selective species. Peltophorum africanum at a fidelity of 47 percent is a preferential species as are the Strychnos spp. (41 percent), which include S. spinosa and S. innocua. Three indifferent species are A. burkei (33 percent), Canthium spinosa (20 percent) and Terminalia phanerophlebia (20 percent). The remaining 26 out of the 31 species recorded are of strange fidelity.

4.2.2.1.5. The Combretum apiculatum Community

The Combretum apiculatum Community embraces the Mixed Closed and Open Woodland that grows on the scarplets and benches of the terraced topography described in Chapter 2.3.1.4. and illustrated by Photo 18. The Closed Woodland growing on the rocky scarplets and which is largely protected

Table 24. Species percentage constancy (C) and fidelity (S) of plants in the Combretum apiculatum Community. Results based on a group of 54 samples.

		C	S
Tall species	Combretum apiculatum	80	40
	Spirostachys africana	72	20
	Ziziphus mucronata	72	13
	Acacia gerrardii	63	18
	A. nilotica	54	11
	A. burkei	44	29
	A. karroo	44	9
	Schotia brachypetala	39	15
	Dombeya rotundifolia	35	23
	A. nigrescens	30	9
	Pappea capensis	28	13
	Sideroxylon inerme	22	15
	A. tortilis	17	4
	Sclerocarya caffra	15	7
	Terminalia phanerophlebia	13	35
Short species	Dichrostachys cinerea	56	14
	Rhus pentheri	48	18
	Tarchonanthus camphoratus	48	20
	Maytenus senegalensis	39	17
	Euclea shimperi	37	13
	A. senegal	35	17
	Grewia monticola	20	22
	Brachylaena ilicifolia	17	10
	Maytenus heterophylla	17	6
	A. caffra	17	11
	Thespesia acutiloba	15	44
	Gardenia spatulifolia	13	18
	Strychnos spp.	13	42
	Ozoroa paniculosa	11	10

SUMMARY

Degree	Percentage range	Quantity of species recorded for each degree of			
		Constancy		Fidelity	
5	80-100	Constantly present	1	Exclusive	0
4	60-79	Mostly present	3	Selective	0
3	40-59	Often present	6	Preferential	3
2	20-39	Seldom	9	Indifferent	6
1	1-19	Rare	10	Strange	20

from fire has already been described as a later stage of the lithosere in Chapter 4.1.2.3. The total extent of the Combretum Closed Woodland and earlier lithoseral communities, as well as the Combretum Open Woodland, is all mapped as Combretum apiculatum Mixed Woodland on the vegetation map because the three types could not be differentiated at the scale used. The remainder of this section is mostly devoted to the Open Woodland, as illustrated by Photo 45, growing on the benches which are covered by stony soils of the Mispah Series (Chapter 2.4.1.).

INSERT PHOTO 45, TABLE 24

The upper stratum of the C. apiculatum Open Woodland consists of trees from five to eight metres tall which can be widely spaced, as in Photo 18, or closely spaced, as in Photo 39, and which are often aggregated into clusters of several trees when neighbouring crowns are in contact or almost so. A lower stratum of short trees and shrubs is not distinct because the plants are often widely separated. A ground layer of grasses on the benches is sufficiently dense for burning, which is not the case on the scarplets. The Themeda-Aristida and Themeda-Panicum are the commonest amongst an assemblage of several grass communities which make up the ground layer.

The composition of the Community is rather variable from one locality to the next depending on local edaphic and climatic differences. Plants of the Acacia burkei Community are particularly noticeable where patches of sand are contained by the Mispah Series; plants of the A. nigrescens or A. nilotica Communities are noticeable under doleritic or poorly drained conditions; and at higher altitudes, above about 300m, plants of the A. caffra Community are conspicuous. The composition of the C. apiculatum Open Woodland, as given in Table 24, includes these variations.

The four most numerous trees of the upper stratum include the dominant C. apiculatum, which is constantly present at 80 percent, and mostly present Spirostachys africana (72 percent), Ziziphus mucronata (72 percent) and Acacia gerrardii (63 percent). Often present trees are A. nilotica (54 percent)

A. burkei (44 percent) and A. karroo (44 percent). Seldom present in the upper stratum are Schotia brachypetala (39 percent), Dombeya rotundifolia (35 percent), A. nigrescens (30 percent), Pappea capensis (28 percent) and Sideroxylon inerme (22 percent). Acacia tortilis (17 percent), Sclerocarya caffra (15 percent) and Terminalia phanerophlebia (13 percent) are rare.

Of the short species composing the lower stratum, Dichrostachys cinerea, Rhus pentheri and Tarchonanthus camphoratus are often present. The remaining short species are seldom or rare.

There are neither exclusive nor selective plants in the Community. Thespesia acutiloba (44 percent), Strychnos spp. (42 percent) and C. apiculatum (40 percent) are preferential, while the remaining species given in Table 24 are indifferent or strange.

4.2.2.2. The Acacia-Spirostachys Closed Woodland Association

4.2.2.2.1. The Acacia nilotica Community

Stands of the Acacia nilotica Community are found on pediments formed over Lower and Middle Ecca shales and on parts of the benches of the terraced topography. Many of the large, 50 ha and more stands shown on the vegetation map correspond with a series of coalescing pediments that constitute the gently undulating country in the Mphafa and Gyoqini catchments. Some large stands are also shown for the Mhlanganobhedu area to the east of the Reserve where they also occur over shale pediments. Small stands of less than one or two hectares found over Middle Ecca shale on the benches are not shown on the vegetation map.

Two soil series are common on the shale pediments occupied by the A. nilotica Community. The Arcadia Series of the Upland Soil Association (Chapter 2.4.1.) develops in situ from the shale, but the Uitvlugt Series of the Bottomland Soil Association (Chapter 2.4.2.) develops from transported materials, including much shale, which accumulate at a toe-slope where the pediment gradually passes into a valley bottom or a stream bank.



Photo 45. A Combretum apiculatum Open Woodland contains a tree of Acacia gerrardii (left) and large-leaved trees of C. apiculatum, several of which are included in a cluster (left, middle distance). A Themeda triandra dominated ground cover of grasses is sufficiently dense for burning. A north aspect bench at Mpila, 9.5.70.



Photo 46. A fairly open Thicket of pale barked, multi-stemmed, evergreen Euclea daphnoides shrubs. A dark leafed, small specimen of Schottia brachypetala is on the extreme left and close to three trees of Acacia nilotica with black trunks. A closely grazed ground layer of the Themeda - Urochloa Community is in the foreground. In the background, a few trees have regenerated on the debris slopes of Zintunzini which was cleared of woody growth over 20 years ago. A Pliocene pediment at Msasaneni, 17.7.70.

The Community is physiognomically very variable. Over the Uitvlugt Series it grows as a Mixed Woodland where small Bush Clumps of Closed Woodland are contained within larger stands of Open Woodland as shown in Photos 26 and 40. The Bush Clumps can be from two metres to 50m in diameter. They are formed by a dense growth of tall species, from five to nine metres tall, and of short species up to about four metres tall. Abandoned termite mounds are found in the centre of Clump (Chapter 4.1.3.2.) and a zone of heavily grazed grasses surrounds the Clump (Photo 26) which is thereby protected from fires which can burn through the dense grass layer of the surrounding Open Woodland (Photo 40). The Open Woodland contains a few, widely separated trees about five metres tall and a few short plants. The grass layer of the Open Woodland, which does not extent into the Clumps, can be of the Themeda-Panicum and the Themeda-Urochloa Communities.

INSERT PHOTOS 46, 47

Over the Arcadia Series, the Bush Clumps are less numerous and the Community sometimes appears to be more uniform. Tree density is, however, still rather variable. The crowns of neighbouring trees may be in contact or separated by as much as thirty metres. But the density of the short species is such that stands of fairly open Thicket develop (Photo 46). The grass layer in these stands is mostly of the Themeda-Urochloa and Panicum coloratum Communities which are often so heavily grazed, as shown in Photo 46, that fire is precluded.

At the lowest lying parts of the pediments, on the toe-slopes, the Community becomes yet denser. The short species in particular close up to form small, dense patches of Thicket (Photos 25, 47). Beyond the toe-slopes the A. nilotica Community grades into Closed Woodland of either the Spirostachys Community on stream banks or the A.grandicornuta Community on alluvial terraces.

The physiognomic variation of the A. nilotica Community is largely explicable on a basis of edaphic, biotic and fire factors. The Uitvlugt soils have a poor internal

Table 25. Species percentage constancy (C) and fidelity (S) of plants in the Acacia nilotica Community. Results based on a group of 45 samples.

		C	S
Tall species	<i>Acacia nilotica</i>	100	16
	<i>Ziziphus mucronata</i>	78	11
	<i>Spirostachys africana</i>	58	13
	<i>A. tortilis</i>	49	9
	<i>A. gerrardii</i>	47	11
	<i>A. karroo</i>	29	10
	<i>A. luederitzii</i>	29	27
	<i>A. nigrescens</i>	27	7
	<i>A. grandicornuta</i>	24	10
	<i>Pappea capensis</i>	22	9
	<i>Schotia brachypetala</i>	22	17
	<i>A. robusta</i>	16	9
	<i>A. burkei</i>	13	7
	<i>Euclea shimperi</i>	53	16
Short species	<i>A. senegal</i>	42	17
	<i>Dichrostachys cinerea</i>	42	9
	<i>E. daphnoides</i>	40	35
	<i>Maytenus cymosus</i>	38	11
	<i>Rhus pentheri</i>	29	9
	<i>Brachylaena ilicifolia</i>	24	13
	<i>E. undulata</i>	24	16
	<i>Tarchonanthus camphoratus</i>	22	8
	<i>Schotia capitata</i>	18	12
	<i>A. borleae</i>	16	37
	<i>Canthium spinosa</i>	11	10

SUMMARY

Degree	Percentage range	Quantity of species recorded in each degree of			
		Constancy		Fidelity	
5	80-100	Constantly present	1	Exclusive	0
4	60-79	Mostly present	1	Selective	0
3	40-59	Often present	7	Preferential	0
2	20-39	Seldom	11	Indifferent	3
1	1-19	Rare	5	Strange	22

drainage and are periodically waterlogged in the rainy season owing to the hard, impermeable B horizon. These soils have, therefore, an effective depth of about 30 cm, confined to the thickness of the A horizon, out of a total depth of about one metre. The waterlogged and shallow soils are not conducive to trees which are generally widely spaced. Termite colonies inhabiting the soils build their mounds above normal ground level (Photo 34) probably to avoid the lower, waterlogged soil horizon during the rainy season. But the termites also make myriads of narrow passages in the B horizon which they presumably inhabit during the dry season. The narrow passages, as well very often as the burrowing activities of antbears, improve the aeration, moisture permeability and effective depth of the soils. These improved soil conditions as well as the protection from fire, as described in Chapter 4.1.3.2., afforded through termite activity encourage a dense woody plant growth, and the Bush Clumps develop on the termite mounds. Outward extension of a Bush Clump to beyond the vicinity of a termite mound is evidently retarded by the unfavourable soil conditions and by the passage of the grass fires which burn through the surrounding Open Woodland.

Tree density increases lower down on the pediments as effective soil depth increases. Waterlogging is less evident, and the number of termite mounds decreases as does the number of Bush Clumps. But the grasses are heavily grazed to the extent that fires are mostly precluded and the Thickets of short species encroach.

INSERT TABLE 25

The composition of the Community is given in Table 25. Of the tall species listed, the following grow singly rather than in the Bush Clumps: Acacia nilotica, which is constantly present at 100 percent, mostly present Zizyphus mucronata (78 percent), often present A. tortilis (49 percent) and A. gerrardii (47 percent) as well as seldom present A. karroo (29 percent) and A. nigrescens (27 percent). The seldom present A. luederitzii (29 percent) is a Thicket constituent (Photo 25). Seldom present A. grandicornuta

(24 percent) occurs where the A. nilotica Community merges into the A. grandicornuta Community: rarely present A. robusta (16 percent) and A. burkei (13 percent) occur where the A. nilotica Community is ecotonal to the A. robusta and A. burkei Communities.

These tall species are the main constituents of the Bush Clumps; often present Spirostachys africana (58 percent), seldom present Pappea capensis (22 percent) and Schotia brachypetala (22 percent). Other tall species of Bush Clumps not included in Table 25 include Sideroxylon inerme, Mimusops africana, Pseudocassine transvaalica and Cussonia spp.

Short species typical of the Bush Clumps include often present Euclea shimperi (53 percent), seldom present Maytenus cymosus (38 percent) and Rhus pentheri (29 percent), rarely present Schotia capitata (18 percent) and Canthium spinosa (11 percent). The other short species listed are most often found as the constituents of Thickets and include often present Dichrostachys cinerea (42 percent) and Euclea daphnoides (40 percent), seldom present Brachylaena ilicifolia (24 percent), Euclea undulata (24 percent) and Tarchonanthus camphoratus (22 percent).

Short, rarely present Acacia borleae forms small, usually less than 50m in diameter, dense stands that contain few other woody plants. Some of these stands are found near the Gunqweni road and on parts of the Khukho and Ntoyiana Hills. The stands of A. borleae grow specifically where internal soil drainage is most severely impeded in the Uitvlugt Series. An impervious, nodular ironstone layer in the soil is responsible for the severely impeded drainage on the Hills.

The A. nilotica Community contains neither exclusive, selective nor preferential species. Three species of indifferent fidelity do, however, bring out some conspicuous features of the Community. Acacia borleae, at a fidelity of 37 percent, grows on the most poorly drained localities; Euclea daphnoides (35 percent) forms extensive stands of fairly open Thicket; and Acacia luederitzii (27 percent) forms small patches of impenetrable Thicket. Many seedlings of A. luederitzii, about one metre high, in the Bizo catchment and some other areas indicate that the extent of Thicket is increasing.

The Community is so variable that it is described and classified with difficulty. It contains areas of both sparsely and densely spaced trees as well as Thicket. The sparsely wooded areas are dominated by the scraggy crowns of A. nilotica made of densely packed, untidy stems bearing large pairs of spines 10 cm and longer. Tall species in the open areas are typical of the Open Woodland Association; they include A. nilotica, A. tortilis, A. gerrardii, A. karroo, A. nigrescens, A. burkei and Zizyphus mucronata. But the tall species, including Spirostachys africana, A. grandicornuta and Pappea capensis, of the Bush Clumps and other densely wooded areas are typical of the Closed Woodland Association. The lack of highly faithful species in the Community indicates that its constituents, apart from A. borleae and E. daphnoides, are well represented amongst other communities.

Although the A. nilotica Community is the characteristic woody vegetation over shale and shale derived soils, its distribution is ecotonal between communities of the Open Woodland Association on soils of the Upland Association and communities of the Closed Woodland Association on soils of the Bottomland Association. Acacia nilotica rarely exceeds five metres in height, and the A. nilotica Community in bottomland sites seems to be seral to the taller, eight or nine metres high, trees of the A. grandicornuta and Spirostachys Communities, as is also indicated by the dominance of S. africana in the Bush Clumps of the A. nilotica Community. The A. nilotica Community has, therefore, been included as part of the Acacia-Spirostachys Closed Woodland Association, rather than the Acacia-Combretum Open Woodland Association. Combretum apiculatum is present in all Communities of the Open Woodland, but is absent from the A. nilotica and other Closed Woodland Communities.

4.2.2.2.2. The Acacia grandicornuta Community

Large stands, several square kilometres in extent, of the Acacia grandicornuta Community shown on the vegetation map cover the alluvial terraces of the Quaternary Surface which lie alongside the Black and White Umfolozi Rivers (Photo 27), and which extend along the lower reaches of the major streams. The Community is virtually exclusive to the deep, highly

Table 26. Species percentage constancy (C) and fidelity (S) of plants in the Acacia grandicornuta Community. Results based on a group of 90 samples.

		C	S
Tall species	<i>Acacia grandicornuta</i>	93	73
	<i>Spirostachys africana</i>	61	26
	<i>Pappea capensis</i>	49	33
	<i>A. tortilis</i>	45	13
	<i>Ziziphus mucronata</i>	31	9
	<i>Boscia albitrunca</i>	25	31
	<i>A. nigrescens</i>	23	14
	<i>A. nilotica</i>	23	9
	<i>A. luederitzii</i>	20	69
	<i>Sideroxylon inerme</i>	15	14
Short species	<i>Schotia brachypetala</i>	15	9
	<i>A. karroo</i>	10	8
	<i>Maytenus cymosus</i>	58	29
	<i>Euclea undulata</i>	47	53
	<i>E. shimperi</i>	35	19
	<i>Schotia capitata</i>	35	40
	<i>Brachylaena ilicifolia</i>	34	33
	<i>Dichrostachys cinerea</i>	29	11
	<i>Canthium setiflorum</i>	29	49
	<i>A. senegal</i>	17	15
	<i>E. daphnoides</i>	13	21
	<i>Tarchonanthus camphoratus</i>	12	8
	<i>Azima tetraacantha</i>	11	24

SUMMARY

Degree	Percentage range	Quantity of species recorded in each degree of			
		Constancy		Fidelity	
5	80-100	Constantly present	1	Exclusive	0
4	60-79	Mostly present	1	Selective	2
3	40-59	Often present	4	Preferential	3
2	20-39	Seldom	10	Indifferent	7
1	1-19	Rare	7	Strange	11

Fertile, orange Doveton, Makatini and Shorrocks soils of the Hutton form (Chapter 2.4.2.).

The Community comprises two distinct strata as shown in Photo 37. Tall species of an upper stratum grow as a Closed Woodland where neighbouring crowns are in contact or fail to meet by about 10m. Slender branched, rather graceful trees of A. grandicornuta dominate at a height of eight metres. A lower stratum of short species is from three to four, rarely five, metres tall. The short species can be widely spaced at about 15m apart, as in Photo 37, but are often densely packed to form a Thicket as in Photo 35. Some of the Thicket stands are in small clearings where the upper stratum is lacking or exceptionally sparse. The sparse Panicum maximum Community (Chapter 4.2.1.2.2.) and the sparse Panicum coloratum Community (Chapter 4.2.1.2.3.) as well as the many forbs of the Bottomland Soil Association (Chapter 4.1.3.1.4.2.) constitute a ground layer.

INSERT TABLE 26

Of the tall species listed in Table 26, which gives the Community composition, constantly present A. grandicornuta (93 percent), mostly present Spirostachys africana (61 percent), seldom present A. nigrescens (23 percent) and rare Schotia brachypetala (15 percent) reach heights of about eight metres. The other tall species include often present Pappea capensis (49 percent) and A. tortilis (45 percent); seldom present Zizyphus mucronata (31 percent), Boscia albitrunca (25 percent), A. nilotica (23 percent) and A. luederitzii (20 percent); as well as rare Sideroxylon inerme (15 percent) and A. karroo (10 percent).

Short species listed in Table 26 include often present Maytenus cymosus (58 percent) and Euclea undulata (47 percent); seldom present Euclea shimperi (35 percent), Schotia capitata (35 percent), Brachylaena ilicifolia (34 percent), Dichrostachys cinerea (29 percent) and Canthium setiflorum (29 percent). Rare species include

A. senegal (17 percent), Euclea daphnoides (13 percent), Tarchonanthus camphoratus (12 percent) and Azima tetraacantha (11 percent).

No species are exclusive to the Community, but A. grandicornuta, at a fidelity of 73 percent, and the Thicket forming A. luederitzii (69 percent) are selective species. Three preferential species are Euclea undulata (53 percent), which forms some Thicket stands containing few other species, Canthium setiflorum (49 percent) and Schotia capitata (40 percent). The other species listed are of indifferent or strange fidelities.

4.2.2.2.3. The Spirostachys africana Community

The distribution of the Spirostachys africana Community, shown on the vegetation map, is along streambanks (Photos 2, 10) and drainage lines (Photo 8). The Community occupies a narrow zone, from a few to about 30m wide, which extends along the drainage lines and streambanks, and which stands out as a dense Closed Woodland that is usually more luxuriant than the surrounding vegetation. The bouldery substrate along the drainage lines (Photo 8) affords considerable protection from fire to the plants which grow in soil pockets between the boulders. Dark grey or black, two and more metre deep soils of the streambanks (Photo 9) include the Bonheim, Rensburg and Sunvalley Series (Chapter 2.4.2.).

The upper stratum of the Community is of strong, straight-boled trees standing to about nine metres tall with their crowns either in contact or spaced about one metre apart. A lower stratum, rarely rising above four or five metres, contains mostly weaker and shorter multi-stemmed plants sometimes aggregated to form small, Thicket-like patches. A sparse ground layer of the Panicum maximum Community (Chapter 4.2.1.2.2.) is present excepting in the most heavily shaded areas where it is replaced by a litter of leaves shed from the woody strata.

Occasional fallen trunks and branches, as well as accumulations of flood debris from several years, on and near the streambanks indicate that fires are rare. Twigs and other organic detritus trapped by living plants of the

Table 27. Species percentage constancy (C) and fidelity (S) of plants in the *Spirostachys africana* Community. Results based on a group of 53 samples.

		C	S
Tall species	<i>Spirostachys africana</i>	83	32
	<i>Schotia brachypetala</i>	68	26
	<i>Pappea capensis</i>	53	24
	<i>Olea africana</i>	49	70
	<i>Sideroxylon inerme</i>	43	28
	<i>Acacia nilotica</i>	36	7
	<i>A. robusta</i>	30	22
	<i>A. nigrescens</i>	28	8
	<i>Euphorbia tirucalli</i>	26	70
	<i>Mimusops africana</i>	26	54
	<i>Ziziphus mucronata</i>	21	4
	<i>Phyllogeiton zeyheri</i>	15	40
	<i>A. tortilis</i>	13	3
	<i>A. burkei</i>	11	7
	<i>A. karroo</i>	11	5
	<i>Terminalia phanerophlebia</i>	11	30
Short species	<i>Euclea shimperi</i>	74	26
	<i>Maytenus cymosus</i>	53	18
	<i>Schotia capitata</i>	38	30
	<i>Brachylaena ilicifolia</i>	32	20
	<i>Tarchonanthus camphoratus</i>	30	12
	<i>Dichrostachys cinerea</i>	25	6
	<i>Diospyros glandulifera</i>	19	56
	<i>Rhus</i> spp.	19	7
	<i>Canthium spinosa</i>	17	32
	<i>Dombeya cymosa</i>	17	47
	<i>Euclea undulata</i>	17	13
	<i>Maytenus undatus</i>	17	56
	<i>Canthium setiflorum</i>	15	16
	<i>Croton menyhartii</i>	13	47
	<i>Aloe marlothii</i>	11	55

SUMMARY

Degree	Percentage range	Quantity of species recorded for each degree of			
		Constancy		Fidelity	
5	80-100	Constantly present	1	Exclusive	0
4	60-79	Mostly present	2	Selective	2
3	40-59	Often present	4	Preferential	7
2	20-39	Seldom	10	Indifferent	10
1	1-19	Rare	14	Strange	12

Community show that flood waters from the streams can flood the Community to depths of two metres. Flooding does not normally last for more than a few hours or a day, but many mature, large, dead trees standing along the Dakaneni Stream near the Black Umfolozi River may have been killed by prolonged waterlogging as a result of the heavy rains and exceptional floods in July, 1963 (Chapter 2.5.5.).

INSERT TABLE 27

The largest of the tall species listed in Table 27, which gives the Community composition, are Spirostachys africana, constantly present at 83 percent, mostly present Schotia brachypetala (68 percent) and seldom present Acacia robusta (30 percent). Other tall or tallish constituents, from five to eight metres high, of the upper stratum include often present Pappea capensis (53 percent), Olea africana (49 percent) and Sideroxylon inerme (43 percent); seldom present species include Acacia nilotica (36 percent), A.nigrescens (28 percent), Euphorbia tirucalli (26 percent), Mimusops africana (26 percent). Notable amongst the rare species are Phyllogeiton zeyheri (15 percent), which has heavily galled branches and bright red berries, and Terminalia phanerophlebia (11 percent) which has pale, yellow-green, translucent leaves and winged fruits.

Few of the short species listed in Table 27 warrant mention. Mostly present Euclea shimperi (74 percent) and often present Maytenus cymosus (53 percent) are the commonest short plants. Seldom present shrubs of Schotia capitata (38 percent) set their attractive red flowers throughout the year.

Exclusive species are lacking from the Community, but two selective species are Olea africana, at a fidelity of 70 percent, and Euphorbia tirucalli (70 percent). Seven preferential species are Maytenus undatus (56 percent), Diospyros glandulifera (56 percent), Aloe marlothii (55 percent), Mimusops africana (54 percent), Dombeya cymosa (47 percent), Croton menyhartii (47 percent) and Phyllogeiton zeyheri (40 percent). The remaining 22 species listed are of indifferent or strange fidelities. Some of the species of higher fidelity,



Photo 47. A dense Thicket includes shrubs of Tarchonanthus camphoratus (left) and Brachylaena ilicifolia (right). A tree of Pseudocassia transvaalica stands higher than the Thicket. Gqolweni, 8.5.70.



Photo 48. A grove of palms in the Phoenix reclinata Community. The spinescent sapling (lower right corner), the protruding twigs (right margin) and some of the large trees (background) are of Acacia robusta. A dense colony of tall Solanaceous weeds has invaded the short ground layer consisting mostly of Cynodon dactylon. Bed of the Fuyeni Stream near its confluence with the White Umfolozi River, 4.4.70.

notably E. tirucalli, D. glandulifera and A. marlothii, as well as some of lower fidelity, such as Terminalia phanerophlebia and Canthium spinosa, are typical lithoseral plants. Their fidelity to the Spirostachys africana Community arises from the inclusion of the rocky drainage lines in the distribution range of the Community. Euphorbia trucalli has a thin bark and is probably one of the few woody species in the Reserve easily damaged by fire when mature. Aloe marlothii also has a thin bark but this is protected from fire by dead, very tough leaves which remain attached to the stem (Photo 1).

4.2.2.3. The Acacia-Ficus Riverine Woodland Association

4.2.2.3.1. The Phoenix reclinata Community

Stands of the Phoenix reclinata Community are present in only three places in the Reserve, in the beds of the Muniwane, Mphafa and Fuyeni Streams; they are confined to small localities stretching upstream for only one or two kilometres from the confluences of the streams with the White Umfolozi River. These localities are periodically inundated, for several days at a time, by stream floods and by water thrown back from high flows in the River; but they are protected from the direct onslaught of floodings in the White Umfolozi. A high water table is present throughout the year in the alluvia of the Riverine Soil Association occupied by the Community (Chapter 2.4.3.).

INSERT PHOTO 48

Groves of palms, as shown in Photos 22 and 48, five metres high constitute the Community. Phoenix reclinata, which has graceful, slightly recurved, evergreen fronds, is the dominant and almost exclusive species present. The Community is seral to the Acacia robusta Community and, apart from the palms, the only other woody species present in any noticeable quantity is A. robusta. A ground layer is made primarily of stoloniferous grasses, including fine Cynodon dactylon and coarse Panicum meyerianum; both grasses have a firm hold on the loose, sandy substrate.

4.2.2.3.2. The Acacia robusta Community



Photo 49.

The trailing, white stems and fine, compound leaves of Acacia brevispica overgrow a simple-leaved shrub of Maytenus senegalensis. One metre tall grasses of Panicum maximum grow protected from grazing and trampling on the shrub perimeter. The over-hanging branch (top right) is of Spirostachys africana. Black Umfolozi River, 9.5.70.

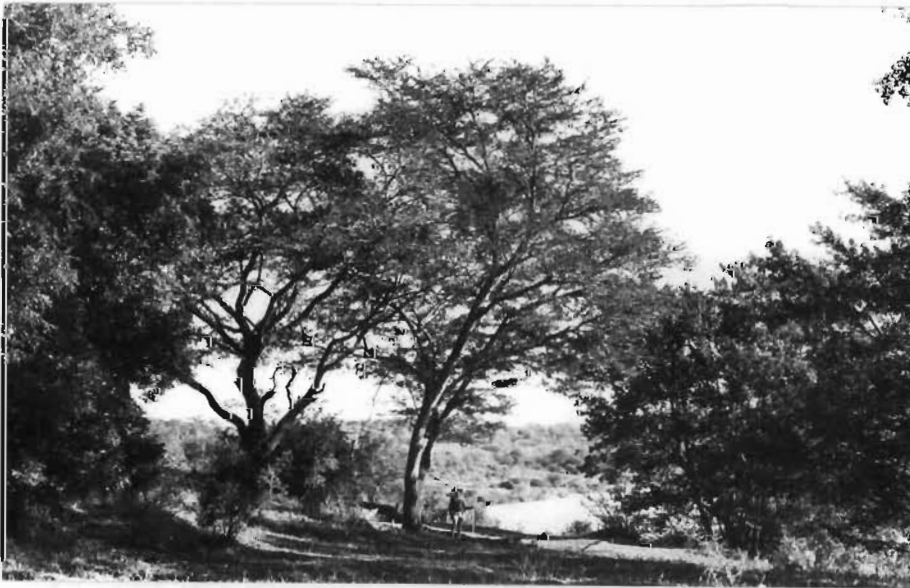


Photo 50.

Two large, 16m tall trees of Acacia robusta occupy the photo centre. Part of a Spirostachys africana tree is on the left; to the right and close to the Black Umfolozi River are several trees of Ficus sycamorus growing four metres lower down the bank than the figure. A lawn-like grass layer is mostly of Cynodon dactylon and Dactyloctenium australe. Mhuzane, 9.5.70.

Table 28. Species percentage constancy (C) and fidelity (S) of woody plants in the Acacia - Ficus Riverine Woodland. Results based on a group of 28 samples.

		C	S
Tall species	Acacia robusta	100	42
	Ziziphus mucronata	57	6
	Ficus sycamorus	50	80
	Spirostachys africana	43	7
	A. tortilis	40	5
	Schotia brachypetala	40	9
	Sideroxylon inerme	17	6
	A. nigrescens	13	2
	A. nilotica	10	1
	Phoenix reclinata	10	75
Short species	Sclerocarya caffra	10	3
	Maytenus senegalensis	60	11
	Azima tetracantha	33	29
	Euclea shimperi	33	7
	Dichrostachys cinerea	30	4
	A. brevispica (climber)	27	73
	Rhus simii	27	25
	Schotia capitata	13	6
	Thespesia acutiloba	13	22
	Canthium spinosa	10	11

SUMMARY

Degree	Percentage range	Quantity of species recorded for each degree of			
		Constancy		Fidelity	
5	80-100	Constantly present	1	Exclusive	1
4	60-79	Mostly present	1	Selective	2
3	40-59	Often present	6	Preferential	1
2	20-39	Seldom	5	Indifferent	3
1	1-19	Rare	8	Strange	13

sycamorus, often present at 50 percent, which tower at heights of about 16m (Photo 50). Other tall species include often present Spirostachys africana (43 percent), A. tortilis (40 percent) and Schotia brachypetala (40 percent). Rare species include Sideroxylon inerme (17 percent), A. nigrescens (13 percent), A. nilotica (10 percent) and Sclerocarya caffra (10 percent), as well as yet rarer trees, not included in Table 28, of Trichilia emetica, Kigelia pinnata and Maerua angolensis. Grasses of Cynodon dactylon and, in the shade, of Dactyloctenium australe make a lawn-like ground layer (Photos 27, 50).

Ficus sycamorus, at a fidelity of 80 percent, is an exclusive species while Phoenix reclinata (75 percent) and Acacia brevispica (73 percent) are selective species almost completely restricted to the Riverine Woodland. Acacia robusta (42 percent) is preferential, and the other species listed are of indifferent or strange fidelities.

The exclusive fidelity of F. sycamorus warrants the inclusion of Ficus in the name of the Acacia-Ficus Riverine Association even though it contributes less to the upper stratum than does the dominant A. robusta. The thick, often one metre or more in diameter, buttressed, yellowish trunks of F. sycamorus are most impressive. The names of the Rivers and of the Reserve possibly derive from the Zulu name for F. sycamorus; Lugg (1949, p 144) writes "Umfolozi is an abbreviation of umfula woluzi - River of Fibre - and so named because of the large quantity of a ficus fig which grows at the junction of the two Umfolozi rivers. The bark is used for making sewing fibre or uluzi." But Mr I. C. Player (pers. com.) contends that the fibre is not obtained from F. sycamorus, and that woluzi is the name of a much smaller tree. The Zulu name for Acacia robusta is mungamanzi which means "the Acacia karroo that grows near water" (Mr I. C. Player, pers. com.).

4.2.2.4. Phenology

Most trees and shrubs in the Reserve react to the dry season by shedding their leaves to the extent that all Woodland Associations in the Reserve are deciduous. The leaves are progressively shed during the vegetational autumn

which starts in April or May, depending on when arid conditions set in. New leaves appear during the vegetational spring which can be from September to November, depending on the commencement of the first rains of the climatic year. The following observations on leaf phenology and the flowering times of some trees and shrubs were made over the period June, 1968, to June, 1969.

A drought experienced during the winter of 1968 was partly relieved on the 9th and 10th of August when 20mm of rain fell. At the end of August, Acacia robusta was the first tree to put out new, green leaves and by September 9th, after a total of 42mm rain had been recorded for the season, was followed by A. burkei, A. gerrardii, A. tortilis, Spirostachys africana, Terminalia phanerophlebia, Dichrostachys cinerea and Commiphora neglecta. In spite of a dry spell between the 10th and 27th of September, during which time the White Umfolozi River stopped flowing, the following species flowered: A. burkei, Euphorbia tirucalli and Pappea capensis, as well as Sclerocarya caffra which also produced new leaves.

Some 100mm of rain recorded during October broke the dry spell and the River again flowed. Many trees which set leaves in humid October included A. grandicornuta, A. karroo, A. luederitzii, A. senegal and Zizyphus mucronata. Humid conditions extended into November, which received 60mm rainfall, when green leaves were produced by A. nigrescens, A. nilotica, A. borleae, Combretum apiculatum, Gardenia spatulifolia, Dombeya cymosa and D. rotundifolia, the latter having flowered several months earlier before its leaves appeared.

All trees and shrubs in the Reserve were in full and luxuriant green leaf by early December, and remained so during December, which received 140mm of rain, and the other summer months of January (30mm), February (19mm) and March (223mm) of 1969. The beneficial effects on the vegetation of the liberal rainfall of March were carried over into April, which is the first month of winter and which received 38mm rainfall; but the effects of drought became apparent in May (25mm rainfall). Towards the end of May the leaves of many trees yellowed and died back; Sclerocarya caffra being amongst the first and Acacia tortilis amongst the last to shed their leaves. Plants growing along drainage lines, stream

and river banks, on rocky scarplets and on steep mesoclines were able, because of better than average soil and rock moisture conditions in these places, to retain green foliage for longer than most plants growing in other places.

By the end of June, which received four millimetres of rain, the majority of woody plants had lost their leaves. Great expanses of grey Woodland characterised by naked, stark and apparently lifeless tree crowns rested in the Reserve during the remaining winter months of July (21mm), August (zero) and the earlier part of September. All the dominant species shed their leaves, whether the leaves were finely divided as in the Acacia spp. or entire as in Spirostachys africana and Combretum apiculatum.

A few species did, however, show a considerable proportion of green during the arid winter months, such as the grey-green succulent stems of Euphorbia tirucalli and Cissus quadrangularis, and the glaucous succulent leaves of Portulacaria afra, Aloe spp. and C. rotundifolia. Short growing woody species which retained many of their leaves in a green condition included Euclea spp., Maytenus spp. and Tarchonanthus camphoratus; while tall growing species included Schotia brachypetala, Olea africana, Pappea capensis, Sideroxylon inerme, Boscia albitrunca and Phoenix reclinata. Some specimens of Ficus sycamorus retained many green leaves, yet others shed the majority of their leaves. All these species which remained conspicuously green during winter had simple leaves or leaves which were not finely divided.

* * * * *

CHAPTER FIVE

BIOTIC FACTORS

5.1. Mammals

5.1.1. Man

5.1.1.1. Habitation

The earliest humans known to have been in the Reserve included nomadic Bushmen who subsisted mainly through hunting. Nothing remains of their occupation apart from some stone artifacts, potsherds and a few rock paintings described by Penner (1970). The Bushmen were gradually displaced by the pastoral Nguni people who arrived in Zululand in about the 16th century or earlier (Bryant, 1929).

The scourge of nagana, an incidence of malaria and, possibly, sleeping sickness endemic to the Reserve until recent times, as well as the turbulence of wars (see Bryant, 1929; Morris, 1966), would likely have discouraged a dense and permanent Nguni population. Several Nguni clans are, however, known to have lived in the Reserve at times from the 18th century or earlier, until the conclusion of the Zulu War in 1879. The Ndwande clan occupied higher-lying parts in the western half of the Reserve, and the Mthetwa clan lived in the eastern area from Mpila to the confluence of the Black and White Umfolozi Rivers (Vincent, 1970, pp 10-12). Traces of Nguni occupation include grinding stones used for the preparation of food and a few earthen smelting furnaces. Pieces of nodular ironstone and ferruginous shale found near the furnaces were probably the ores used in smelting. Outcroppings of these rock types are visible in the Reserve at several places including Ntoiyiyana and Nselwini; the ironstone at Ntoiyiyana has been excavated presumably for use as an ore.

Very few people have lived in the Reserve since 1880. Several campsites occupied at times during the anti-nagana campaign from 1929 to 1952 are marked by rubble, by a secondary growth of Dichrostachys cinerea and, occasionally, by an exotic Opuntia sp. The present day permanent population of about 100 comprises conservation personnel and their families. In addition as many as 50 tourists can be

accommodated.

5.1.1.2. Management

Current management activities include : the construction of a rhinoceros-proof fence along the east, south and west boundaries; the shooting, or capture and removal, of surplus animals; anti-poaching patrols; the burning of fire breaks; and soil reclamation works in some of the more badly eroded areas. Services are provided by way of staff housing, tourist camps - one at Mpila and one near Masimba, electricity and roads. But services are kept to a minimum in the Wilderness which is a specially protected area occupying the southern portion of the Reserve. Motor vehicles are largely precluded from the Wilderness and access is usually by foot or horseback. Some of the roads, including disused tracks in the Wilderness, cause soil erosion where they are incorrectly aligned or inadequately drained.

An important annual event in August or September is the burning off of grasses in various areas of the Reserve in an attempt to simulate the effects of fires started by lightning. Fires started by lightning during olden times, before the days of roads and fire breaks, were able to travel great distances (see Bayer, 1955, p 547). The important effects of fire in removing the dead litter of grasses, in stimulating vernal aspect forbs, and in suppressing invasion by woody plants have been described in Chapter 4.1.3.1.5. Each part of the Reserve is, theoretically, burned once in a three or five year cycle. In practice, only the upland areas which contain sufficient litter are actually burned; the bottomland areas cannot be burned because there is insufficient litter for firing. The presence of many young woody invaders in some upland areas, as shown in Photos 32 and 33, indicates that fires have not been sufficiently frequent in recent years to suppress invasion even though the grass is sufficiently rank for burning. An encroachment by Thicket forming species in most bottomland areas, as shown in Photos 35 and 47, is partly attributable to the absence or rarity of fires in the bottomlands during recent times.

However, the maturity of some Thicket plants in

the bottomlands, as exemplified by Photo 25, indicates that they may have established some twenty or more years ago. Some Thickets would have existed in rocky areas and in overgrazed places before the turn of this century even though lightning-started fires took place, and in spite of the fires which were intentionally set by early hunters as a means for attracting game to the flush of grasses which follows burning (Vincent, 1970 p 18). The use of fire for veld management is recorded by Vincent (1970, p 19) for the period between 1911 and 1932; but he notes that very little burning was done during the 1930's because of the danger to many wooden-framed Harris fly traps placed all over the Reserve. The strong possibility of some Thicket stands having been initiated during that period, about forty years ago when burning was discouraged, is supported by the opinion of Mr. W. Foster, a Game Conservator who was familiar with the area from 1906 to 1955. Vincent (1970, p 17) writes that Foster "expressed concern at the increased bush encroachment in and around the reserve since the advent of the Veterinary Division in their mission to exterminate the tsetse fly".

Some research recently started by Mr. R. Porter in the Reserve aims at monitoring the effects of present burning management on the vegetation.

5.1.1.3. Cultivation

No signs were found of any small gardens which the early Nguni inhabitants probably prepared for growing grain crops. A few small patches used for maize cultivation by personnel engaged on anti-nagana activities during the 1930's were pointed out to the author by Mr. Mqoyi Nkosi. These patches have now a grass cover but contain more plants of Dichrostachys cinerea than would normally be expected.

Most exotic species in the Reserve, apart from some tended in camp gardens, are the weeds characteristic of cultivated fields. Some of the weeds are carried in by floods of the Black and White Umfolozi Rivers; and the wider diversity of weed species is found on their banks. The exotics although abundant in some places, such as around the camps and on old paths, are unlikely to spread so much that

their control becomes a problem, Opuntia sp. possibly being the only exception. The following exotics, amongst others, were recorded:

<u>Erigeron bonariense</u>	<u>Opuntia</u> sp.
<u>Bidens pilosa</u>	<u>Melia azaderach</u> (a tree)
<u>Tagetes minuta</u>	<u>Argemone</u> sp.
<u>Zinnia multiflora</u>	<u>Datura stramonium</u>
<u>Alternanthera pungens</u>	<u>Solanum</u> spp.
<u>Ricinus communis</u>	Chenopodiaceae (several spp.)

5.1.2. Wild animals

5.1.2.1. Status of species

A rich and varied population of wild mammals in the Reserve long survived the hunting activities of Bushmen and the Nguni people. However, the arrival of European hunters and the introduction of firearms in about 1850 soon took a toll of the animals. Much legal and illegal hunting took place at various times (see Chapter 1.1.) even after the Reserve was initially proclaimed in 1897.

Between 1880 and 1925 some nine large animal species were eliminated. Eland were eliminated by 1880 but were re-introduced in 1964. Elephant were shot out by about 1890. In 1915 the last lion was shot; in 1958 a lion was again seen and about 60 are now present. By 1925 the following species had vanished: giraffe (re-introduced in 1955) and cheetah (re-introduced in 1966) as well as these four species which, together with elephant, have remained absent - wild dog, brown hyaena, oribi and hippopotamus (Vincent, 1970).

The loss of elephants from the Reserve is particularly noteworthy because they probably played a rôle in the distribution of some plant seeds, particularly when the fruits are large or hard, as for example in Kigelia pinnata, Strychnos spp., and Sclerocarya caffra, and are not easily eaten by birds. The fruits of Strychnos spp. and S. caffra are, however, also opened and devoured by other animals, including wild pig, baboon and monkey. Germination may well be promoted after the seeds have passed through the digestive

Table 29. Estimates of large herbivore biomasses of past and present populations in Umfolozi Game Reserve. Data for period 1929 to 1967 based on Mentis (1970), and for 1972 on Hitchins (1972).

		Biomasses in kg /km ²			
		1929	1942	1967	1972
Grazers	Species				
	Buffalo	43	470	356	657
	Reedbuck	14	101	86	13
	Mountain reedbuck	<1	66	<1	2
	White rhinoceros	240	720	2750	4731
	Warthog	74	136	198	58
	Waterbuck	75	112	368	277
	Wildebeest	87	121	610	534
	Zebra	2260	257	140	286
	Sub-totals grazers	2794	1983	4508	6558
Mixed feeders	Bushbuck	45	302	51	<1
	Bushpig	5	18	12	-
	Eland	-	-	10	<1
	Impala	-	1	51	95
	Klipspringer	-	<1	<1	-
	Nyala	-	3	137	118
	Steenbuck	3	<1	<1	<1
	Sub-totals mixed feeders	53	327	263	215
Browsers	Duiker	24	35	18	<1
	Giraffe	-	-	14	32
	Kudu	27	114	122	152
	Black rhinoceros	6	14	68	51
	Sub-totals browsers	57	163	222	235
GRAND TOTALS		2904	2473	4993	7008

tracts of these animals (see Phillips, 1925). Any high elephant concentrations in the past might have maintained a more open condition than is seen at present in the Woodlands (see Laws, 1970).

From 1929 to 1952 an intensive campaign was waged against tsetse flies, Glossina spp., which are vectors of the trypanosomes responsible for nagana. This campaign involved at least three operations.

The first operation was conducted over two periods, from June 1929 until November 1930, and from December 1942 until April 1950. The first operation initially aimed at confining all game animals within the Reserve, but later attempted a total destruction of all game that might supply blood food for the tsetse fly; the black and the white rhinoceros were amongst the few species not intended for destruction. A record was kept of the animals shot through counting the tails returned by hunters; over 70,200 animals were shot in the Reserve and its immediate surroundings during the second period of the first operation alone (Mentis, 1970, pp 371-372). Some game animals survived in spite of the slaughter and these survivors, together with more recent immigrants, have multiplied most successfully so that game animals are again plentiful. The rich diversity of mammal species now present is illustrated by Appendix III which is a list of the 39 larger mammals in the Reserve kindly supplied by Mr. O. Bourquin.

INSERT APPENDIX III AT BACK OF BOOK

INSERT TABLE 29

An idea of some changes in the large herbivore biomass, as well as the extent of population increases since the anti-nagana shootings, over the last 43 years is given by Table 29. The Table gives large herbivore biomasses in the Reserve as estimated by Mentis (1970) for the years 1929 and 1942, being the times when the slaughter periods started, and for 1967 which is seventeen years after the last slaughter. Biomass data included for 1972 are based on the results of a census taken during August (Hitchins, 1972).

Table 29 shows a three-fold increase, from 2,473 kg/km² in 1942 to 7,008 kg/km² in 1972, in the total herbivore biomass. The grazing animals, which constitute the bulk of the large herbivore biomass, have more than trebled from 1,983 to 6,558 kg/km² over the same period. The biomass of browsers has increased by fifty percent since 1942. A decrease shown for the same period in mixed feeders is probably not of much significance; mixed feeders are not easily enumerated during a census because they tend to be concealed by dense woody growth. The data in Table 29 are, however, sufficiently accurate to indicate that considerably larger amounts of grass and of browse are being removed at present than were removed some forty years ago.

In 1929, zebra at 2,260 kg/km² constituted the bulk of the grazing biomass but have since declined to the present low value of 286 kg/km². But the white rhinoceros has increased over this period from 240 to 4,731 kg/km². The zebra is a grazer of coarse, climax grasses, but the white rhinoceros feeds off finer, mid-seral and pioneer grasses. Table 29 indicates that the grazing demand for climax grasses has declined whilst that for mid-seral and pioneer grasses has increased.

5.1.2.2. Grazing

5.1.2.2.1. Grass requirements

An empirical estimate of the amount of dry food material required during a year by all the individuals of a herbivorous species in the Reserve is obtainable from the following formula, based on the recommendations of Mr. M. Mentis (pers. com.) and of Tainton and Downing (1971).

$$e = a \frac{x b}{1000} \times \frac{c}{d}$$

where

- a = metabolic weight of the species obtained by raising the mean body weight in kg to the index 0.72;
- b = the number of individuals of the species;
- c = dry material intake of one mature livestock unit for one year, equivalent to 3,320 kg in Acacia Woodland;

- d = the metabolic weight of one mature livestock unit, equivalent to $454^{0.73}$ kg;
 e = estimated dry material intake of the species for one year in metric tonnes.

The wild herbivore food requirements estimated by use of the formula depend on comparisons with data on the dry grass intake of a mature, domestic livestock unit living in Acacia Woodland; the data being supplied by Mr. N.Schoeman (pers. com.) of the Animal Husbandry Department, University of Natal. The comparisons are not, however, entirely accurate for several reasons. The basic metabolic rate of a highly active, free-ranging wild herbivore will be higher than that of a passive, quieter, domestic beast; the wild herbivore will thus need more food for its maintenance. Yet further amounts of food will likely be required by the wild herbivore which possibly has a lower digestive efficiency than a domestic beast of equivalent body weight; the domestic beast has been specially bred for the efficient conversion of food into energy. Furthermore, the numbers of mixed feeders and of the smaller-sized grazers, such as nyala, bushbuck and warthog, were under-counted during the 1972 aerial census because poor weather and dense bush restricted visibility; but the counts of buffalo, zebra, white rhinoceros and wildebeest are probably quite accurate (see Hitchins, 1972). Taken overall, the food requirements of the wild herbivores obtained by use of the formula are, therefore, probably under-estimates, and are thus regarded as the minimal dry food requirements.

The formula was applied for the main herbivorous species, based on the numbers obtained during the 1972 population census (Hitchins, 1972) and the results are presented in Table 30. The species are grouped in Table 30 according to their feeding behaviour, whether as mainly being the grazers of uplands, the grazers of bottomlands, the mixed feeders which are nearly always found on bottomlands, or as browsers. The mean body weights, metabolic weights and numbers of the herbivores are entered in columns 1, 2 and 3; and the estimated total dry food needs are in column 4. The entries in column 5 for the estimated dry grass needs are similar to those in column 4 for the grazing species; but have

Table 30. The mean body weights, metabolic weights and numbers of herbivores in Umfolozi Game Reserve during 1972, as well as their estimated, minimal total dry food and dry grass requirements. See text.

		1	2	3	4	5
Species		Mean body weight, kg	Metabolic weight, kg	Numbers	Total food needs, tonnes	Dry grass needs, tonnes
Grazers on upland	Buffalo	499	92.0	649	2278	2278
	Reedbuck	54	18.4	118	83	83
	Mountain reedbuck	23	9.8	39	15	15
	Zebra	215	50.2	657	1259	1259
					Sub-total	3635
Grazers on bottomland	White rhinoceros	1723	229.6	1336	11910	11910
	Warthog	30	11.8	950	429	429
	Waterbuck	204	47.8	669	1219	1219
	Wildebeest	181	44.5	1454	2436	2436
					Sub-total	15994
Mixed feeders on bottomland	Bushbuck	30	11.8	7	3	2
	Eland	385	76.5	1	3	2
	Impala	41	15.0	1136	649	325
	Nyala	73	22.8	795	692	346
	Steenbuck	11	5.7	7	2	1
					Sub-total	676
Browsers	Duiker	11	5.7	10	2	0
	Giraffe	680	116.3	23	102	0
	Kudu	136	35.9	550	753	0
	Black rhinoceros	816	133.1	31	158	0
					Sub-total	0
GRAND TOTAL						20305

been reduced by about 50 percent for the mixed feeders. The reduction was made because grasses make up about one half of the total diet of the mixed feeders; in summer the mixed feeders eat 80 percent grass and 20 percent browse, but in winter take 20 percent grass and 80 percent browse (Messrs J. Vincent and J. Anderson, pers. com.). Column 5 reflects a zero dry grass need for the browsing species which consume negligible quantities of grass.

INSERT TABLE 30

Table 30 shows that the minimal dry grass requirement for all the larger herbivores in the Reserve during 1972 totals an estimated 20,305 tonnes. The herbivores having the greatest grass requirements are the white rhinoceros, which at 11,910 tonnes takes up 59 percent of the total grass requirement; followed by the wildebeest at 2,436 tonnes, equivalent to 12 percent of the total; by buffalo at 2,278 tonnes (11 percent); zebra at 1,259 tonnes (6 percent); and waterbuck at 1,219 tonnes (6 percent). The other herbivores, such as nyala and warthog, require much smaller quantities of grass, even if their numbers were grossly under-estimated during the 1972 census, compared with the animals having estimated minimal requirements of over 2,000 tonnes per annum. These comparisons of the grass requirements of the herbivores should not be regarded as precise because physiological differences of the various species are not accounted for. The data are, however, probably adequate for broad comparisons. Data presently available on the feeding behaviour, digestive physiology and energy utilisation of herbivore species represented in the Reserve are insufficient for more accurate determinations.

5.1.2.2.2. Grazing behaviour and grass productivity

The estimated minimal dry grass requirements of the herbivores in 1972 as given in Table 30 totals 20,305 tonnes. Of the total, a minor portion of 3,635 tonnes is obtained from the uplands and the balance of 16,670 tonnes from the bottomlands. This means that each one of the 24,600 hectares constituting the uplands must produce 148 kg/ha/yr of dry grass in order to supply the wants of the upland grazers. Each one of the 24,600

hectares of the bottomlands must produce 678 kg of dry grass per year to supply the grazers and mixed feeders of the bottomlands. The grass demands from the uplands and the bottomlands can be compared against the 1,000 kg which is believed to be within the annual grass production capability of one hectare of Acacia Woodland in an "average" condition (Dr. P. Theron, pers. com.); accurately determined data on the grass productivity of Acacia Woodland are not known to be available for any place in Southern Africa.

Approximately one half of the Reserve's area, comprising the entire extent of the Miocene Surface as well as the hills and most ridges of the Pliocene Surface, forms the uplands. The uplands are largely occupied by the Open Woodland Association and by the Grassland which are mostly characterised by the dense, rank grasses of the Themeda and the Themeda-Panicum Communities which are so lightly grazed, as mentioned in Chapter 4.2.1.2. and illustrated by Photos 17 and 40, that the excess ungrazed portions could easily be burned off annually. The only herbivores which readily graze these rank grass communities are buffalo, zebra, reedbuck and mountain reedbuck, which together comprise only about 16 percent of the total grazing biomass. The other grazers tend to avoid the upland grazing although they occasionally do use it - wildebeest more so than the rest of them. The estimated grass productivity of 1,000 kg/ha/year on the uplands is, therefore, well able to meet the grass demand of 148 kg/ha/year calculated for the upland grazers.

The remaining 84 percent of the grazing biomass, including the white rhinoceros, wildebeest, waterbuck and warthog, as well as the mixed feeders, particularly the nyala, bushbuck and impala, depend largely or almost entirely on the bottomland areas for the bulk of their grass supplies. The bottomlands, comprising the entirety of the Quaternary Surface, the valleys and most of the pediments of the Pliocene Surface, make up the other half of the Reserve, about 24,600 ha in extent. It is doubtful whether the bottomlands are able to fully supply the 678 kg/ha/year of grass calculated as being the minimal requirement of the herbivores dependent on the bottomlands.

The present productivity of the sparse bottom-land grasses is probably considerably lower than the estimated 1,000kg/ha/year possible because the grass cover is definitely in a much poorer than "average" condition. The actual productivity of the grasses could well be almost equivalent to the weight of grass removed by grazing, whether the calculated 678 kg/ha/year or some other weight, because there is so little surplus grass left over from grazing at the end of winter that the veld cannot be burned. The herbivores have so strong a preference for the bottomlands that these areas are persistently grazed, throughout the year and from one year to the next, such that the grasses never receive the occasional rest believed essential for maintaining grass vigour in the summer, low rainfall regions of Southern Africa (see West, 1955, pp 627-629). The sparse, from 10 to 16 percent cover of the Panicum coloratum and Panicum maximum Communities, being the main grass Communities of the Closed Woodland Association which occupies the bottomlands, is not therefore surprising. These Communities, described in Chapter 4.2.1.2. and illustrated by Photos 37 and 38, are the most heavily grazed in the Reserve at pressures from 47 to 80 percent. There is little doubt that the grass removed exceeds much more than one half of the possible annual grass production of 1,000 kg/ha, and this will lead to yet further deterioration of the grass cover in the bottomlands. West (1955, p 628) states that a removal of between 40 and 50 percent of the annual production is sufficient to deplete grass reserves and cause damage to the veld.

Some differences in soil fertility would seem to explain why the most heavily grazed areas in the Reserve, including the Panicum coloratum and P. maximum Communities, should be concentrated in the bottomlands, and why the least grazed areas, including the Themeda and Themeda-Panicum Communities should be on the uplands. Experimental evidence, given in Chapter 3.4.4. and summarised in Fig. 5, showed that the grasses sampled from the carbonate rich, illuviated clay soils of the Bottomland Association contained a higher nutrient content than the grasses from the less fertile, eluviated clay soils of the Upland Association. Domestic

livestock in Natal are believed to seek out pasturage having the highest nutritional status (Mr. R. Ludorf, pers. com.). The same evidently applies in the Reserve where herbivores prefer the grasses on the bottomlands, which have the higher nutrient content, to the grasses on the uplands which have the lower nutrient content.

Some research recently started in the Reserve by Mr. R. Porter aims at providing additional and more detailed information on the amounts of grass produced and the amounts removed by grazing, as well as an assessment of grass behaviour under current grazing pressures.

5.1.2.3. Browsing

The main animals requiring browse in the Reserve are listed in Table 29. Little is known about the food requirements of these animals and their effects on the woody vegetation because their browsing activities were not fully studied. The larger animals, including giraffe, kudu, eland, black rhino, nyala and bushbuck, that can reach food two or more metres above ground have an advantage over the other, smaller animals listed in Table 29 which have a lower reach. Giraffe can browse tree tops beyond the reach of other herbivores (Photo 3); they seemingly prefer to eat Acacia spp. but, by confining their movements within areas of the Open Woodland, do not take advantage of the many Acacia spp. trees in the Closed Woodland. Kudu and eland are wide ranging and were not noticed to have any particular food preferences. On the other hand, black rhinoceros were nearly always found in Closed Woodland where their favourite browse plants included Acacia spp. and Spirostachys africana, which is sometimes so heavily used that many smaller specimens are maintained in a pruned condition permanently within rhinoceros reach (Photo 51). Nyala and bushbuck are also mostly confined to Closed Woodland where the amount of browse available is not as plentiful as would appear at first sight because many of the encroaching and lower stratum woody plants consist of Euclea spp., which were never found to have been browsed, as well as Brachylaena ilicifolia, Maytenus spp., and Tarchonanthus camphoratus which were rarely seen browsed.



Photo 51. Heavy browsing by animals such as black rhinoceros, kudu, nyala and impala has stunted the growth of these Spirostachys africana saplings. The dense growth of individual specimens is due to constant coppicing. The close spacing of the individuals is due to the rarity or absence of fire. In the background is a tree of Acacia tortilis. Gqoyini, 9.5.70.



Photo 52. The thick, fire-protective bark of Spirostachys africana was probably gnawed away by porcupine. The exposed heart wood shows signs of subsequent damage by fire and insects. In the background, a Thicket grows on a rocky scarplet protected from fire. Mbuzane, 9.5.70.

Apart from the preceding species, which are regarded as being amongst the least palatable of woody plants in the Reserve, most other species may be browsed to a greater or lesser extent. The most heavily browsed included Xeromphis rudis and Jasminum multipartitum which were often dwarfed and pollarded shrubs cropped to within a few decimetres of the ground. Other favoured browse plants included Zizyphus mucronata and Boscia albitrunca.

INSERT PHOTO 51

5.1.2.4. Other activities

Porcupine gnaw the bark of trees, particularly of Spirostachys africana and to a lesser extent of Schotia brachypetala and of Acacia caffra, to a height of about 50 cm above ground level (Photo 52). No completely ring-barked trees were noticed, but removal of the thick, protective bark exposes the tree trunks to insect and fire damage (Photo 52). Such damage may account for some of the dead trees occasionally found in the Reserve.

INSERT PHOTOS 52, 53

Apart from the extensive trampling done to bottomland soils by the herbivores, many intensively trampled game paths extend across the Reserve. Some of the paths are so well used that they have in places been trampled one or two decimetres below normal ground level. The paths are devoid of herbage but do not result in much erosion except where they cross stream banks.

The burrows tunnelled by antbear, subsequently enlarged by warthog and later formed into small pans through the wallowing action of animals, mostly rhinoceros, are described in Chapter 2.2.1. Heavy grazing and trampling reduce grass cover around the pans (Photo 13).

White rhinoceros tend to consistently defecate at certain selected localities such that numerous dung middens are scattered throughout the Reserve (Photo 53). Black rhinoceros also behave in this way. The rhinoceros habitually



Photo 53. The one metre long marker is at the centre of a rhinoceros dung midden. Few plants, mostly annual weeds, grow around the heavily trampled midden. A game path leads away from the midden into the background. To the right, a Thicket grows along the edge of a rocky outcrop. Mphafa, 10.5.70.

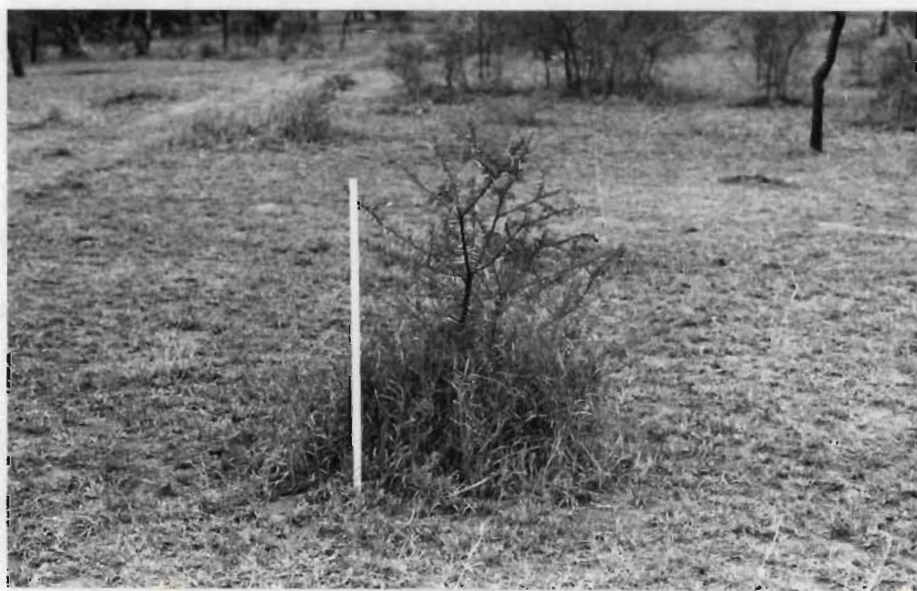


Photo 54. A small patch of Themeda triandra survives where protected from grazing under a spinescent Acacia tortilis sapling. A short and sparse stand of the heavily grazed Panicum coloratum Community surrounding the sapling is too sparse for burning. Note the encroachment by other saplings in the background. Pilocene pediment at Msasaneni, 17.7.60.

kick their dung about and make such a disturbance that few plants grow on the organic rich dung middens. Some plants found on the perimeter of middens or in abandoned middens include a few grasses, Cynodon dactylon, Eleusine indica and Chloris spp., and rather more weeds including Gomphrena celosoides, Alternanthera pungens, Aizoon glinoides, Datura stramonium and other Solanaceae. Insectivorous birds, notably the hadedah ibis, seek coprophilous insects attracted to the middens.

5.2. Insects and birds

The second operation of the anti-nagana campaign took place from 1932 to 1952 when several areas in the Reserve were kept clear of trees and shrubs. Although many woody plants have since regenerated, the extent of the clearings is still visible in the three areas, namely: a strip of land about three kilometres wide that extends along the entire length of the western boundary of the Reserve; an almost rectangular 800 ha area of the Mfulamkhulu catchment adjacent to the White Umfolozi River; and a 20m wide belt that extends several kilometres between the summits of Matshemnyama and Matshemhlope. The principle of clearing trees was based on an idea of R.H.T.P. Harris that tsetse flies would not cross strips of land devoid of trees, and that cleared areas could be used for preventing dispersal of the flies; the idea of clearing was, however, abandoned after Glossina pallidipes, an inhabitant of Grassland and Open Woodland, was found to cross the cleared strips (Prof. Bayer, pers. com.). The extent of shaded, sandy areas needed by G. pallidipes and G. brevipalpis, an inhabitant of densely wooded areas, for breeding purposes would have been slightly reduced through the clearing of trees (see Bayer, 1938, p 431).

Insecticides used during the third operation of the anti-nagana campaign finally eliminated the flies. Extensive spraying of the insecticides was at first done from Anson bomber-aircraft, but later on the permanent breeding areas of the flies were sprayed from helicopters (Prof. Bayer, pers. com.). Dichlor-diphenyl-triclorethane was sprayed in 1947; and from 1948 until August 1951, benzahexachloride was intermittently sprayed (Vincent 1970, p 41).

Many different kinds of insects are found in the Reserve even though the insecticides were used. The more conspicuous insects include termites which are active in many parts, particularly the Madlozi catchment. Termites were seen to remove fair quantities of dead grass during winter. The amount of grass removed by the termites is regarded as being insignificant in comparison with that grazed by game. The importance of fire-free zones, as well as the improved soil permeability, in and around termite mounds have already been mentioned in connection with the establishment of woody seedlings and the development of Bush Clumps (Chapters 4.1.3.2. and 4.2.2.2.1.). The termites also destroy a certain amount of dead plant debris which falls to the ground. For instance, nearly all traces of some dead Acacia nigrescens and Commiphora spp. stems, up to 15 cm in diameter, deliberately left on the ground in Open Woodland at Thobothi had vanished within three years because of termite activity. The termites seem, however, to be less active in Closed Woodland where fallen trunks appear to lie for longer periods.

Mr. T. Oatley, ornithologist of the Natal Parks Board who has compiled a checklist of over 200 bird species presently known from the Reserve (unpublished records of the Natal Parks Board), is of the opinion that predatory birds in the Reserve, which might well have been adversely affected by the insecticides, have since recovered. He has not noticed any major difference between the predatory bird population in the Reserve and that in surrounding areas which were not sprayed. The effects of the insecticides on insects, insectivorous birds and other animals are not fully known because wildlife in the Reserve was not studied for this purpose either before or after use of the insecticides (Vincent, 1970, p 41).

Frugivorous birds in the Reserve, such as doves, loeries, barbets, bulbuls, starlings and white-eyes, are important distributors of some plant seeds. These birds are particularly attracted to figs, as in Ficus spp., and other fleshy fruits, as borne by the following species amongst others:

<u>Olea africana</u>	<u>Pappea capensis</u>
<u>Mimusops africana</u>	<u>Garcinia livingstonei</u>
<u>Sideroxylon inerme</u>	<u>Dovyalis caffra</u>
<u>Euclea</u> spp.	<u>Commiphora</u> spp.

Plant seeds which have passed through the digestive tracts of the birds may well germinate sooner than those which have not (see Phillips, 1928). The birds are, therefore, probably important agents in the woody succession of the Reserve through promoting the distribution and germination of seeds in much the same way as described by Phillips (1931) for the Knysna Region.

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CHAPTER SIX

DISCUSSION AND CONCLUSIONS

6.1. Physiognomic categories

6.1.1. Phenology

Nearly all plants in the Reserve, apart from the few succulent species, respond to the sub-humid to almost arid winter climate when dry atmospheric conditions prevail (Chapter 2.5.6.), and when severe soil moisture deficiencies are experienced over the greater area of the Reserve on upland and bottomland soils.

The majority of woody plants respond by shedding their leaves even though this may happen later in the season (or to a slightly lesser extent) where soil moisture is plentiful as in the riverine soils, or is better than average as on the rocky scarplets, or where comparatively mesic conditions are experienced as on the steep, south-east aspects (Chapter 4.2.2.4.). All the Woodland Associations in the Reserve have, therefore, a fairly similar deciduous phenology. Climatic conditions are so dry, even in the comparatively mesic places, that the succession of Thicket or of Woodland to Forest is precluded. The Forests so typical of many south aspects in Natal, such as on the Hlabisa Heights (north of the Black Umfolozi River) which receive almost double the mean annual rainfall of the Reserve, are not represented in the Reserve.

The aerial portions of the grasses also respond to the highly seasonal climate by dying back in winter (Chapter 4.1.3.1.4.). The dead grass litter so produced every year, and probably produced for millions of years, has made possible the occurrence of fire as a fairly regular feature of the landscape. Were it not for an evolutionary involvement of fire, it is unlikely that the majority of tree species in the Reserve and most of Natal would have possessed a bark so well adapted to withstand fire. Neither would be so numerous the several hundred vernal aspect forb species associated with grassland in Natal which are largely dependent for their survival on a periodic removal of the grass litter by spring burnings.

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However, the number of vernal aspect forbs found in dense grass areas on uplands in the Reserve was disappointingly low. It could be, therefore, that these areas have not been burned sufficiently often in recent times, and that many vernal aspect plants, which might otherwise have been present, have been eliminated. The depredations of baboon, porcupine and other animals known to dig out the roots, bulbs, corms, and other swollen underground organs typical of geophytes may also account, but to a lesser degree than infrequent burnings, for the low number of spring aspect forbs.

The contrasting, extraordinarily profuse density of autumnal aspect forbs found on the poorly grassed bottomland soils is also ascribed to an infrequency of fire, but for different reasons. Persistent and heavy grazing in the bottomlands has so depleted the grass cover that insufficient litter remains for firing. The absence of fire is ideal for proliferation of the fire-intolerant, autumnal aspect forbs.

6.1.2. Distribution

The widest tree spacings from about 10 to 60m and sometimes more, in the Reserve, are found in the Open Woodland and in the Grassland. The smallest trees, rarely exceeding six metres in height (except in Acacia nigrescens) and having crown diameters of about five metres, are also found in the Open Woodland and in the Grassland. The distribution of the Open Woodland and Grassland closely corresponds with the distribution of the shallow, leached and often stony Upland Soil Association which has a low moisture storage capacity and which receives the smallest volume of rainwater runoff (see Chapter 2.4.1.).

The most closely spaced tree crowns, at about three metres apart, are in the Closed Woodland Association where the trees are larger, at about seven metres tall and having crown diameters slightly wider than five metres, than in the Open Woodland. The greater extent of the Closed Woodland corresponds with the distribution of the deep, illuviated Bottomland Soil Association which probably has a slightly higher moisture storage capacity, and which receives greater volumes of rainwater runoff, than the Upland Soil Association (Chapter 2.4.2.).

Tree spacing is particularly variable in the Riverine Woodland Association which contains by far the largest trees at about 16m tall and with crown diameters of about 10m. The Riverine Woodland Association is confined to the deep, sandy alluvia of the Riverine Soil Association which has the highest moisture storage capacity of all soils in the Reserve, and which receives the greatest volumes of rainwater runoff.

The distribution of the physiognomic features corresponds so closely with the soil associations, as described above, that the effects of some soil factors will be included for consideration when tree size and woody plant density are discussed below.

6.1.3. Tree size

The largest trees are found on the Riverine soils where the greatest amount of soil moisture is available, and the smallest trees are found on the Upland soils where the least moisture is available. Trees growing on the Bottomland soils, which receive and store more moisture, are slightly larger than trees on the Upland soils, which receive and store less moisture. Low soil moisture content seems therefore to be a factor that limits tree size in the Open and Closed Woodlands compared with the Riverine Woodland. The limiting effects of soil moisture are further demonstrated by slight size differences shown by adjacent open and closed stands in areas of Mixed Woodland where local differences in soil moisture are brought about by geological and biotic factors. For instance, the larger trees of the Closed Woodland growing on the scarplets of terraced topography benefit from the additional moisture supplied by the aquiferous Middle Ecca sandstone, and from the additional moisture supplied by precipitation which gathers on the rock faces (Chapter 2.3.1.4); smaller trees growing on the adjacent benches do not receive such additional moisture supplies. A further example is provided by the larger trees of Bush Clumps which benefit from an improvement in soil moisture capacity brought about through the actions of termites and antbears (Chapter 4.2.2.2.1.); the smaller trees in adjacent stands of Open Woodland contend with effectively shallow soils having both a lower moisture permeability and a lower storage capacity.

Tree size is evidently less affected by soil depth than by soil moisture. Soil depth is indirectly of importance insofar as it determines soil moisture capacity. The increases seen in tree size from the Open to the Closed to the Riverine Woodland seem due more to increases in soil moisture storage capacity than to actual increases in soil depth. Trees on the rocky scarplets (which have virtually no depth of soil) grow larger, because of the additional moisture supplies, than trees growing nearby on one or two metres of soil.

Soil fertility does not affect tree size in the Reserve to the same extent as does soil moisture. The large size of trees on the illuviated Bottomland soils compared with the smaller trees on the eluviated Upland soils could partially be due to the higher Bottomland fertility. But the largest trees of all are on the damp, sandy Riverine soils which are strongly leached and which cannot hold as much plant nutrient as the dry, illuviated, more fertile clays of the Bottomland soils. The larger trees on the rocky scarplets likewise experience less fertile conditions than the smaller trees growing under more fertile, but drier conditions on the adjacent benches.

The stunting of trees and shrubs brought about by browsing (Chapter 5.1.2.3.) and the coppicing brought about through burning (Chapter 4.1.3.2.) are of a minor nature and are not regarded as being significant in determining tree and shrub size.

6.1.4. Woody plant density

Local differences in moisture are reflected by woody plant density. The densest growths of woody plants in the Reserve are the Thickets which grow on steep, south-east aspects which experience more humid atmospheric conditions than other parts. The higher tree and shrub density of Closed Woodland on Bottomland soils is partly ascribable to the greater amounts of soil moisture available there compared with the lesser amounts available to the Open Woodland on Upland soils. The dense growth on rocky scarplets benefits from better moisture conditions than exist on the less heavily wooded benches. Woody growth in Riverine Woodland

is generally less dense than is expected in view of the high moisture content of the alluvia; the irregular pattern of tree densities might be the result of exceptionally strong floods. Mr. N. Steele recorded the loss of many large trees from river banks during a flood (Chapter 2.2.2.). Insufficient time has elapsed for the development of Riverine Woodland on recently deposited alluvia - hence the rather bare expanses of sand as found on some slip-off slopes and on other recently formed banks.

The considerably higher tree and shrub density of Closed Woodland on the deeper, illuviated Bottomland soils, compared with the lower densities on the leached, shallow Upland soils and on the leached, deep Riverine soils, suggests that the higher density is partly due to the higher fertility in the Bottomlands. Although this may well be the case to some extent, the yet higher densities on leached rocky scarp-lets and bouldery debris slopes indicate that the incidence of fire probably prevails over both soil fertility and moisture in determining density as is explained below.

Protection from fire long afforded, probably for thousands of years, by the stony places as well as the lack of competition from grasses, allows for the easy establishment of woody seedlings (Chapter 4.1.3.2.) and for the subsequent development of Closed Woodland or Thicket in rocky places. Fires which periodically burn along the more fertile benches of terraced topography discourage a dense woody growth as is found on adjacent, less fertile but fire protected scarplets. Similarly, protection from fire on and near termite mounds helps permit development of the dense, Thicket-like Bush Clumps; whereas occasional fires in surrounding areas, which would enjoy much the same soil fertility, limit density to an open condition (Chapter 4.2.2.2.1.)

Thickets which have long existed in the Reserve on the steep, south-east aspects, on the rocky places and in the Bush Clumps, are regarded as being of a primary origin. But the extent of most other Thickets, or scrub encroached areas, typical of the Closed Woodland on bottomland soils is regarded as a fairly recent, secondary development arising from a lower incidence, or even exclusion, of fires which would likely have been more frequent in earlier times.

The probable origin of some secondary Thicket

development during the 1930's, when man tried to prevent burning of the Reserve, is mentioned in Chapter 5.1.1.2. Even more secondary Thicket has probably been initiated during the last twenty years as a consequence of the substantial increases in grazing herbivore biomass as enumerated in Table 29. Grasses in the bottomlands have been tremendously depleted, to the extent that fires are not possible in most bottomland areas, because of the excessively large amounts of fodder required by the larger number of grazers, and because of their strong preference for grasses on the fertile bottomlands (Chapter 5.1.2.2.). And so expands the extent of secondary Thicket.

Soil fertility is, therefore an indirectly important factor in promoting secondary Thicket development through its influence on grazing behaviour; but fertility is evidently of no significance in the development of primary Thicket.

6.2. Woody Communities

6.2.1. Floristics

6.2.1.1. Fidelity

Table 31 is a convenient summary, abstracted from Tables 20 to 28, of the characteristic species in each community which have fidelity values of 40 percent and more. Table 31 shows a general paucity of highly faithful species, the more so in the Open than in the Closed or Riverine Woodlands. Of the Open Woodland, the Acacia tortilis Community has no characteristic species at all; and the other open communities contain but one or two selective or preferential species. In the Closed Woodland the Acacia nilotica Community has no characteristic species; this is the most variable and least easily defined Community in the Reserve which is physiognomically, floristically and spatially ecotonal between the other communities of the Closed Woodland and the communities of the Open Woodland. The denser, more easily defined Acacia grandicornuta and Spirostachys africana Communities of the Closed Woodland contain one or two selective and several preferential species. The only community in the Reserve to contain an exclusive species is the Riverine Woodland which has, in addition, two selective and one preferential species.

Table 31. A list of the characteristic species in each Woodland Community summarised from Tables 20 to 28. Only species having a fidelity of 40 percent and more are included.

	Species percentage fidelity						
	Open Woodland					Closed Woodland	Riverine Woodland
	C. apiculatum	Acacia caffra	A. tortilis	A. burkei	A. nigrescens	A. nilotica A. grandicornuta Spirostachys africana	
Thespesia acutiloba	44						
Combretum apiculatum	40						
Acacia caffra		64					
Ozoroa paniculosa		50					
Ormocarpum trichocarpum		44					
Peltophorum africanum				47			
Acacia nigrescens					52		
Acacia grandicornuta						73	
A. luederitzii						69	
Euclea undulata						53	
Canthium setiflorum						49	
Azima tetracantha						46	
Euphorbia tirucalli							70
Olea africana							70
Diospyros glandulifera							56
Maytenus undatus							56
Aloe marlothii							55
Mimusops africana							54
Dombeya cymosa							47
Croton menyhartii							47
Phyllogeiton zeyheri							40
Ficus sycamorus							80
Phoenix reclinata							75
Acacia brevispica							73
Acacia robusta							42

INSERT TABLE 31

Each of the 25 species listed in Table 31 probably depends to a greater or lesser extent, depending on the degree of fidelity, for its successful growth on the rather specific environmental conditions offered by its peculiar habitat. The relevant environmental conditions are outlined in Chapter 4.2.2. Most of the other species in the Reserve, not included by Table 31 and which are of indifferent or strange fidelities, must have a fairly wide ecological amplitude tolerant of a wide range of the environmental conditions presented.

6.2.1.2. Constancy

Figure 7 is used to summarise some of the main features of species constancy as provided by Tables 20 to 28. The Figure was made by listing, in the left hand column, the five more constantly present tree species in each community. The percentage constancy values for these species are represented under the relevant column for all communities in which they are present. Percentage constancy is represented by drawing horizontal lines of such length that one millimetre is equivalent to one percent. The less constantly present trees, and also shrubs, are omitted from the Figure for purposes of brevity because they make a lesser contribution to the communities than do the more numerous and larger trees of the uppermost stratum which include the dominants.

INSERT FIGURE 7

Figure 7 shows that the more constant trees are most often present in more than one community. Several of the trees, Zizyphus mucronata, Acacia nilotica and A. tortilis, are the most abundant in the Reserve and are well represented throughout all three Woodland Associations. Schotia brachypetala is also found throughout excepting in the Acacia caffra Community. These four are included amongst the trees having the widest ecological amplitude. The majority of the other major trees, such as Spirostachys africana, Acacia karoo, A. nigrescens, A. gerrardii, Sclerocarya caffra and Pappea capensis, are present in at least two out of the

three Associations. The floristic similarities mentioned above, as well as others not shown in Fig. 7 but evident from a comparison of Tables 20 to 28, indicate that the three Woodland Associations are part of the same Woodland Formation as was earlier indicated on a phenological basis: Climate is evidently more influential than edaphic factors in determining overall floristic composition of vegetation in the Reserve.

A minority of species having a rather restricted presence does bring out some environmental similarities and differences between the habitats occupied by the Woodland Associations.

Combretum apiculatum is confined to the Open Woodland and indicates the shallow soils and stony conditions typical of uplands and of rock outcrops. Much the same applies to Sclerocarya caffra (but which is also found on deep riverine alluvia), Acacia gerrardii (also on deep soils occupied by the ecotonal A. nilotica Community, to Ozoroa paniculosa and to A. caffra.

The deep, fertile bottomland soils are indicated by a prevalence in the Closed Woodland of Spirostachys africana and, to a lesser extent, by Acacia grandicornuta, Olea africana, Sideroxylon inerme and Acacia robusta. Spirostachys africana is, however, also an indicator of better than average moisture as shown by its presence on rocky scarplets and riverine alluvia. The very moist conditions of the riverine alluvia are indicated by the prevalence of Ficus sycamorus and A. robusta in the Riverine Woodland.

Sharp floristic differences are rarely found neither between the three Woodland Associations nor between the constituent communities within any one association. The main floristic differences, as illustrated by Fig. 7, between the constituent communities of an association exist in often somewhat small differences in the percentage constancy values of the same few species, rather than in the absolute presence or absence of a single species.

An idea of floristic homogeneity in the various communities, and in the Reserve as a whole, is obtainable from Table 32. The Table lists for each community, and the whole Reserve, the percentages of species present in each of the five "degrees of constancy". The Table includes those commoner species having constancies of ten percent and more, as given

Table 32. Percentage of species from each community, and from the Reserve as a whole, present in each degree of constancy. The degrees of constancy correspond with degrees of frequency and are comparable against Raunkiaer's Normal frequency distribution, and Raunkiaer's Law, as given by Oosting (1956) and stated at the foot of the Table.

Community	Percentage of species present in each degree of constancy (frequency)					Total number species present
	C5 1-19	C4 20-39	C3 40-59	C2 60-79	C1 80-100	
Acacia caffra	64	12	14	5	5	43
Acacia tortilis	75	15	2	2	6	52
Acacia nigrescens	73	13	8	4	2	52
Acacia burkei	65	23	5	5	2	57
Combretum apiculatum	70	14	9	5	2	66
Acacia nilotica	57	24	15	2	2	46
A. grandicornuta	33	10	4	1	1	56
Spirostachys africana	70	18	7	3	2	60
Riverine Woodland	74	10	12	2	2	50
WHOLE RESERVE	37	46	12	4	1	109
Raunkiaer's Normal distribution	53	14	9	8	16	
Raunkiaer's Law	C5	> C4	> C3	≡	C2	< C1

in Tables 20-28, as well as the rarer species having lower constancies and which were omitted from Tables 20-28 for purposes of brevity. The five "degrees of constancy" correspond with the five "degrees of presence" as laid down by Braun-Blanquet (1932, p 53), and also correspond with the five "classes of frequency" mentioned by Oosting (1956, p 61). Inserted at the foot of Table 32 are (i) the normal frequency distribution discovered by Raunkiaer, and (ii) a formula expressing Raunkiaer's Law of Frequency (Oosting, 1956, p 61).

INSERT TABLE 32

A comparison of the data in Table 32 shows that the frequency distribution within the communities, and for the whole Reserve, agrees neither with Raunkiaer's Normal nor with Raunkiaer's Law. An exception is in the Acacia tortilis Community which does obey the Law because it is the only Community in the Reserve to contain more constantly present species (Class C_1) than mostly present species (Class C_2).

The failure of most of the Umfolozi data to comply with Raunkiaer's Law is an indication of low levels of floristic homogeneity except in the Acacia tortilis Community, which could well be the most homogeneous in the Reserve. The large proportions of species given for Class C_5 in the Reserve are evidently fairly normal of world vegetation; but the very low proportions of species given for Class C_1 are extraordinarily low in comparison with the Normal, and indicate that homogeneity levels are exceptionally low in the Reserve (see Oosting, 1956, pp 61-62). Table 32 also shows that about one half of the total number of 109 species recorded during sampling can occur in any one of the communities. The levels of homogeneity in the Reserve may, however, not be all that low on a world basis if Raunkiaer did not include samples from Acacia Woodland when determining his Normal distribution.

6.2.2. Succession

The scarcity of sharp floristic differences and the closely similar social status of many species, excepting those of characteristic fidelity listed in Table 31, from one community to the next often makes difficult the field identi-

fication of some communities in the Open and the Closed Woodlands. The similarities in composition between the communities show that woody plant succession is fairly similar in the Open and the Closed Woodlands. The following quotation from Bayer (1938, p 421) on thornveld, or Acacia Woodland, is applicable to the Open and Closed Woodlands in the Reserve. The quotation explains the woody plant succession, suggests why the communities are floristically rather similar and often difficult to identify in the field, and explains the low levels of homogeneity as shown from Table 32.

"Thorn veld is one of the most difficult types of vegetation with which the plant ecologist has to deal. Competition between species is not as severe as in closed types of vegetation, and apart from the effects of fire, the biota is of relatively less importance in determining survival than are physical factors. Any tree species which is adapted to withstand fire and the physical conditions of the environment may become a successful invader of grassland.

Furthermore, local climatic and edaphic factors are subject to greater fluctuations than is the case in closed types of vegetation. Consequently, invasion of grassland by thorn veld species takes place in a comparatively indiscriminate and haphazard manner, and results in the production of a community in which nearly all individuals are of approximately equivalent social status. There is, therefore, often considerable lack of uniformity in the composition of thorn veld communities, and differentiation of the various communities is sometimes a difficult matter."

The denser of the Closed Woodland communities in the Reserve, namely the Spirostachys africana and Acacia grandicornuta Communities are therefore more consistent in composition and more easily recognised because greater competition from a higher plant density enforces a more orderly succession; only the taller growing species which have seedlings tolerant of partly shaded conditions can rise to dominance and persist in the community. The same does not apply to the generally less dense Acacia nilotica Community of the Closed Woodland, and to the much sparser Open Woodland communities, where almost any tall or short growing woody plant can succeed to maturity provided fire damage is avoided during the early stages of development.

Local differences in micro-climate and soil do, however, affect the woody succession in areas which are exposed to burning so that certain favoured species have a greater numerical success than others in any one area. This favouritism is largely responsible for the differences in the percentage constancy values of a species seen from one community to the next in the Open and Closed Woodlands (Fig.7). The most favoured woody species in a locality becomes the dominant of the Woodland community which invades and gradually emerges above the Grassland, as outlined in Fig. 6.

Seedlings and saplings of the woody plant which will become the dominant are represented amongst the earliest woody invaders of the Grassland. Few changes in composition seem to take place either during or after development of the community. The community appears to be fully developed when most individuals of the dominant trees, whether Combretum apiculatum, Acacia tortilis, A. burkei, A. nigrescens, A. grandicornuta or Spirostachys africana, have grown to mature size. The communities dominated by the preceding trees can, therefore, be regarded as the climax consociations of the relevant associations, whether of the Acacia-Combretum Open Woodland or the Acacia-Spirostachys Closed Woodland. The status of the communities dominated by either Acacia caffra or A. nilotica is not so certain; these two very variable communities may well be seral to later stages dominated by taller trees, and could be regarded therefore as consociates rather than as consociations.

6.2.3. Pattern

The pattern of the areas occupied by the communities in the Reserve is largely determined by topography and the distribution of the various rock and soil types, as shown by the correlation given in Table 1. The operation of these physical factors in any one habitat produces the environmental conditions most favourable to the particular tree which will succeed as the community dominant.

The pattern of the distributional relationships between the dominants and their habitats is obtainable if an idealised traverse is taken across part of the Reserve. A traverse taken from a river bank and extending upwards to the

summit of a high hill would show the following sequence of dominants and habitats:

Acacia robusta on the riverbank; A. grandicornuta on an adjacent alluvial terrace; Spirostachys africana on a streambank; A. nilotica on a shale pediment, or A. nigrescens on a dolerite pediment, or A. burkei on a sandstone pediment; A. tortilis on hill tops; and finally, Acacia caffra (sometimes A. karroo) at the summit of the high hill. A number of such traverses in the Reserve would reveal a similar pattern of the dominant trees in each kind of habitat.

The pattern of dominants and habitats given above is reminiscent of the vegetation-soil catena concept developed by Morison, Hoyle and Hope-Simpson (1948). If a catena is present in the Reserve it is partly obscured by the irregular, broken topography and by the complex distribution of the geological substrata wrought by faulting and by the erratic distribution of dolerites. The possibility of the Reserve forming part of a catena embracing a larger area of Zululand should not, however, be ruled out.

Micro-climate also affects the altitudinal distribution of two dominants in the Reserve. Acacia caffra is rarely found below 300m altitude; occurrences below this level are confined to steep, mesic south aspects. Acacia nigrescens is very rarely seen at altitudes above 145m, and is most extensive on gently sloping, xeric north aspects. Climatic conditions in the Reserve would appear to be just within the tolerance ranges of these two species. The Reserve is in fact given by Ross (1971, p 35) as the southern limit of the distribution of A. nigrescens. The altitudinal range in the Reserve, extending from 45 to 579m, seems too small to fully reflect an altitudinal zonation of dominant Acacia species described by Bayer (1938, pp 421-422) for Thornveld.

6.3. Grass Communities

6.3.1. Succession and fire

The grass communities extending over nearly all parts of the Reserve are most conspicuous when seen as the rank Themeda triandra dominated stands of Grassland found on the high hills of the Miocene Surface. Regular burnings, at two or three yearly intervals, of the grasses in late winter,

when they are still in the pale brown and yellow condition of drought, maintain the Grassland by suppressing woody plant invasion. The Grassland is therefore regarded as a fire maintained, sub-climax part of the Deciduous Woodland Formation. Apart from suppressing woody growth, the burnings are necessary for perpetuation of grass vigour (Chapter 4.1.3.1.5.). Fire also seems to be essential for promoting the germination of T.triandra seedlings. Mr. Winston Trollop has kindly allowed me to report the unpublished results of his recent field experiment. No seedlings of T.triandra were discovered in a plot from which the grass litter had been removed by mowing; but numerous seedlings were found during the same period of observation in a nearby plot from which the litter had, on the same day, been removed by burning (W.Trollop, pers.com.).

Themeda triandra is also normally a dominant or co-dominant, except when it has been eliminated through grazing or the absence of fire, where the grass communities are less conspicuous in the ground layer of the Woodland. The succession of short pioneer grasses, followed by mid-seral grasses of medium height, and final dominance by rank, climax grasses in the Woodland is repetitive of that in the Grassland. Local, smallish differences seen in the composition of the communities are ascribable to differences in the environment. For instance, shade thrown by the woody invaders in Woodland modifies the succession so that a greater proportion of shade tolerant grasses, such as Panicum spp., Diplachne eleusine, Enteropogon monostachyos and Dactyloctenium australe, are represented than in the Grassland. The presence of a sandy topsoil encourages a greater diversity of species, notably of Aristida, of Sporobolus and of Eragrostis, than is found when the succession takes place on a clay topsoil. Coarse Cymbopogon validus is more abundant on mesic aspects than elsewhere.

6.3.2. Retrogression and grazing

An abundant grass cover often reported for the decade ending in 1959 (unpublished records of the Natal Parks Board) contrasts markedly with the poor cover presently extensive on the clay soils of the bottomlands. An evident reduction of the past rank grass cover, probably characterised

by climax species, to the present sparse condition characterised by early and pioneer species, is in accordance with the threefold increase in large herbivore biomass estimated over the period 1942 to 1972 (Table 29). The larger grazing biomass of today would remove far greater quantities of grass than were removed thirty years ago so that a reduction in cover is only to be expected. The grazing demand for grasses is, however, low on the upland soils where the grass communities have remained in a climax condition probably little changed compared with their condition thirty years ago. But the very heavy demand resulting from selective grazing, estimated to remove more than 678 kg/ha/yr of grass, on the bottomlands is believed to be well in excess of the amount which can be safely removed without damaging the plants (Chapter 5.1.2.2.). The consequences of over-grazing in the bottomlands have been a drastic reduction in cover and a replacement of Tall, climax species by short, mid-seral and early grasses such that the normal trends of succession have been reversed. The grass communities in the bottomlands at present can, therefore, be described as having been brought about by a retrogression.

The retrogression takes place because the tall, climax species are more severely depleted at each grazing than the short mid-seral or early grasses which are able to withstand greater intensities of grazing (Chapter 4.2.1.2.3.). Persistent grazing eventually eliminates the tall climax species and, because of an accompanying reduction in competition, the short mid-seral and early grasses are able to proliferate. Only a few climax grass plants survive in the bottomlands, but these are mostly confined to patches where protected from grazing (Photo 54).

INSERT PHOTO 54

The effects of heavy grazing and retrogression are also illustrated by Photo 20, where a dense stand of the Themeda-Panicum Community in the foreground is sharply separated by the boundary fence from a sparse stand of the Panicum coloratum Community. The differences between the two stands must be largely due to differences arising from grazing because climatic, topographic and edaphic conditions are

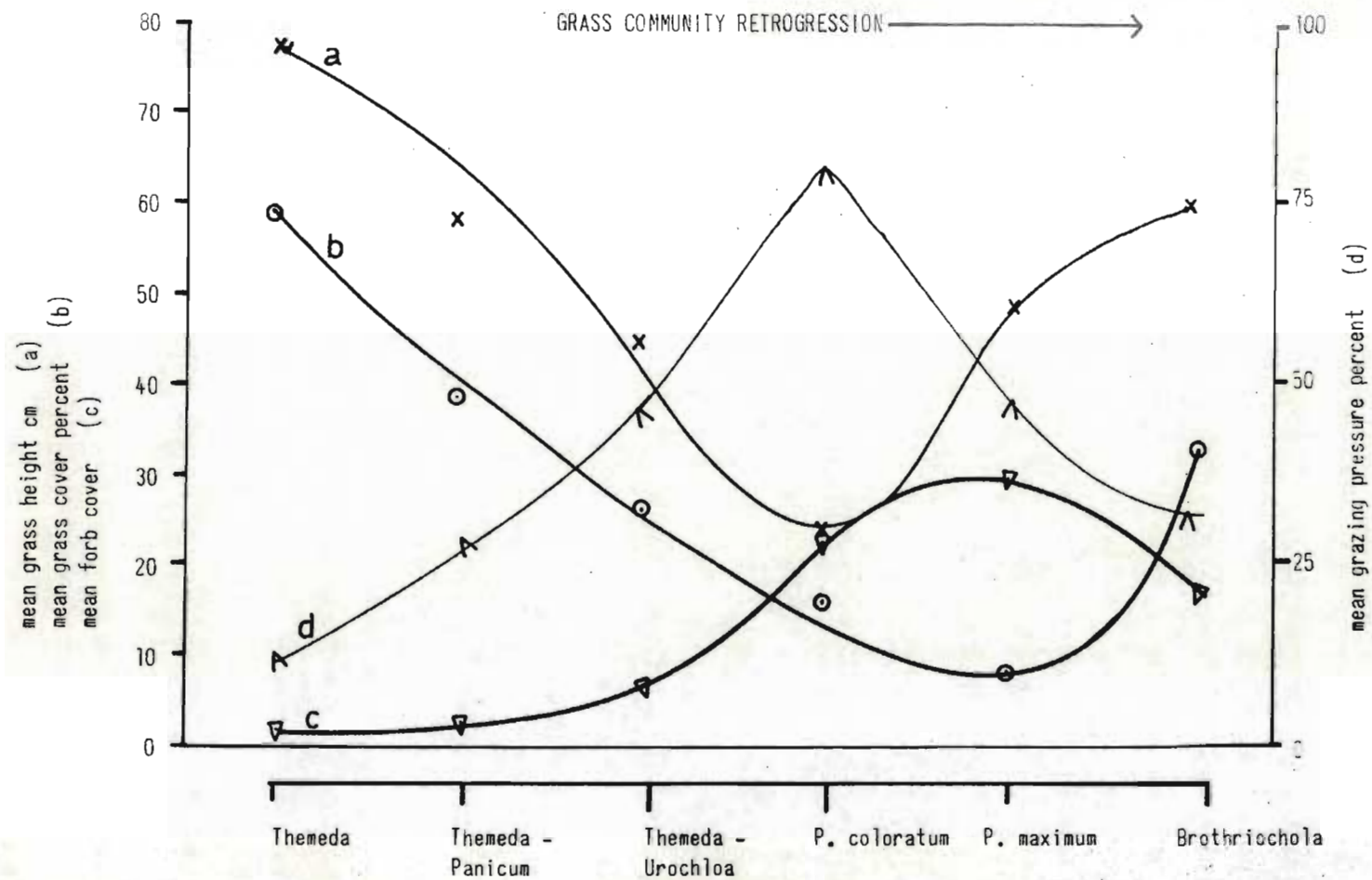


Fig. 8. The retrogressive relationship between grass height (a), grass cover (b), forb cover (c), and grazing pressure (d) in Claysoil Grass Communities. See text.

similar for both the stands.

INSERT FIG. 8

The trends of retrogression and the reaction of the grass communities to grazing will be explained by reference to Figure 8. Only the communities growing on clay soils are considered because they are much more extensive and important from a grazing point of view than those on sandy soils. The Claysoil Communities were arranged along the horizontal axis of Figure 8 according to their retrogressive sequence. The Themeda Community was placed first on the left because it is the least retrograde; it contains the greatest presence of climax grasses and the lowest presence of early grasses. The other communities were placed successively to the right as the proportions of climax grasses decrease and the proportions of early grasses increase as the retrogression proceeds. The most retrograde, Bothriochloa Community which contains the greatest presence of early grasses and the lowest of climax grasses, was placed at the extreme right. The proportions of climax, mid-seral and early grasses present in each of the communities were obtained from Tables 14 - 19. Values obtained from Table 9 on mean grass height (a), mean grass cover (b), mean forb cover (c) and mean grazing pressure (d) are plotted for each of the communities along the vertical axes.

Starting on the left of Figure 8 with the Themeda Community and moving to the right as far as the Panicum coloratum Community, a sixfold increase in grazing pressure (d) from 13 to 80 percent is accompanied by large declines in grass height (a), from 78 to 24 cm, and in grass cover (b) from 59 to 16 percent. The declines are accompanied by a gradual decrease in competition from the climax grasses which are gradually replaced by the mid-seral grasses. The mid-seral grasses become predominant when retrogression reaches the stage represented by the Panicum coloratum Community. The decrease in competition is also accompanied by a rise in the amount of the early grasses, which in the P. coloratum Community have a greater presence than have the climax grasses.

A critical point in the retrogression is reached somewhere between the stages represented by the Themeda-Urochloa and the Panicum coloratum Communities. At this

point competition from the grasses is so low that the percentage forb cover (d) rises sharply to exceed the percentage grass cover. Large increases in grazing pressure and decreases in grass competition before the critical point resulted in comparatively small increases in forb cover. The critical point of the retrogression is evidently reached when the most important of the climax stage grasses in the Reserve, Themeda triandra, is eliminated through excessive grazing.

Persistent grazing of the Themeda-Urochloa and the Panicum coloratum Communities, which contain large proportions of the stoloniferous grasses so highly prized by the white rhinoceros, keeps the grass cover so sparse that burning is impossible at any time of the year (Photo 38). The replacement of grazed-out T. triandra plants by new seedlings is seemingly precluded by a prolonged absence of fire; a fire stimulus is evidently essential before its seeds will germinate (Chapter 6.3.1.).

Some changes in the retrogressive pattern are shown by Figure 8 for the interval between the Panicum coloratum and P. maximum Communities. The mid-seral grasses predominant in the Panicum coloratum Community are, apart from Urochloa mossambicensis, eventually grazed and trampled out; the early stage grasses are also reduced in number. Grass cover falls to a lowest value of 10 percent in the retrogression represented by the Panicum maximum Community, and forb cover rises to a highest value of 30 percent. The combined ground cover of the grasses and the forbs gives the soil insufficient protection from erosion so that sheet and gully erosion set in. Grazing pressure falls off, from a highest value of 80 percent in the Panicum coloratum Community, to a much lower value of 47 percent in the Panicum maximum Community simply because there is almost no grazing available from the very sparse grass cover at 10 percent. But the lack of competition from the sparse grasses and the absence of fires permits invasion by many shrubs and trees. Some tall growing, shade loving, palatable climax species, notably P. maximum and P. deustum, are able to re-establish in the shelter from grazing provided by the woody invaders. An increase in grass height, from 24 cm at the Panicum coloratum Community to 50 cm at the Panicum maximum Community, is therefore shown in Figure 8.

The incidence of the woody invaders which reduces the area available for grazing is also responsible in part for the reduction in the grazing pressure. Note, however, that Themeda triandra has not re-established because fire is absent.

The beginnings of grass recovery are indicated in the retrogression at a point between the Panicum maximum and Bothriochloa Communities. Table 14 shows the presence of the several early stage species which colonise bare areas in the Bothriochloa Community. A few somewhat taller but unpalatable, mid-seral grasses of Aristida congesta and Eragrostis capensis also succeed. The yet taller, but highly unpalatable, climax grass Bothriochloa insculpta becomes dominant. Figure 8 shows, therefore, a continued increase in grass height and a regeneration of grass cover during the interval between the Panicum maximum and the Bothriochloa Communities. The increases in grass height and cover suppress the forb cover which is reduced from 30 to 18 percent. But grazing pressure continues to decline, from 47 percent to 32 percent, as the highly unpalatable B. insculpta rises to dominance. Until such time when Themeda triandra appears in areas dominated by B. insculpta, which has not as yet happened, the Bothriochloa Community should be regarded as being retrograde even though its grasses are recovering from the strains imposed by over-grazing during earlier stages of the retrogression.

Sufficient grazing is being supplied at present to the herbivores because no significant die-off as a result of starvation was noticed. But the grazing is being supplied at the expense of a deteriorating grass cover in the bottomlands because of the selective grazing there. The future capability of the bottomlands to supply adequate grazing under the current grazing pressures is rather doubtful, unless grass retrogression is arrested, particularly in view of the erratic rainfall pattern. Although white rhinoceros and other grazers will take the rank upland grasses when the preferred, short grasses in the bottomlands are scarce, most mixed feeders such as nyala and bushbuck are unlikely to leave the shelter of Closed Woodland on the bottomlands because of their secretive nature. A prolonged, several year period of below average rainfall might well result in such a reduced grass production that herbivore

used in this study suggested that a quantity of 531 samples might be adequate for investigation of vegetation in the Reserve (i.e. one sample for each of 531 landscape units); and showed where the samples might be advantageously distributed (i.e. one sample near the centre of each landscape unit).

Only 516 of the total 531 landscape units were in fact sampled and included for analysis; the balance of 15, being situated in inaccessible places, were omitted. This omission did not greatly detract from the results excepting that quantitative data were not produced for lithoseral communities growing on inaccessible scarps. An allowance of two or more samples, instead of the one sample allotted, per landscape unit could have been made if greater accuracy was desired of vegetation analysis.

Distribution of the samples through use of the landscape unit approach seemed an efficient way for obtaining sample coverage of the large area of the Reserve by a comparatively modest quantity of 516 samples. Were the same quantity of samples to have been distributed at random or systematically, the more extensive communities may have been over-represented and the less extensive communities under-represented. Use of the landscape unit approach at least allowed the evident range of vegetation physiognomic types, and the range of evident landscape physiographic types, to be included amongst the samples.

An objection to the use of the landscape unit approach might be that bias is introduced. Classification structure might have been imposed upon the vegetation, and preconceived ideas might have been formed on possible relationships between plant and habitat.

The extent to which the structure might have been imposed upon the vegetation would have depended largely on the photo-interpretative skill of the investigator, and on the degree of consistence applied whilst delineating landscape features on the airphotos. For these reasons photo-interpretation was repeated in this study after the investigator had become more familiar with the landscape features as a result of considerable field experience. Some landscape unit boundaries were altered as a result of the second and, presumably, more accurate photo-interpretation.

Delineation of the landscape into units dependent on some selected landscape features need not have biased postulations on relationships between plant and habitat. The landscape features of vegetation physiognomy, landform, gradient, aspect, etc., selected for delineation purposes were not directly included for vegetation analysis. Vegetation analysis was based on species presence and absence data; species presence and absence were not incorporated amongst the features used for landscape unit delineation in this study. Neither were any ecological relationships necessarily presumed to exist between the vegetation and other landscape features selected for delineation. It was the function of vegetation analysis and field examination, done after landscape unit delineation and sampling, to suggest which environmental factors might have been of ecological importance to the plant communities, irrespective of whether these environmental features were, or were not, amongst those selected for delineation of the landscape.

The landscape unit approach does not seem, therefore, to depart significantly from the concepts laid down by Lambert and Dale (1964, pp 64-65) for the statistical treatment of vegetation, except that the samples are not taken at random or systematically. Samples taken according to the landscape unit approach could be regarded as stratified samples which are stratified according to selected landscape features evident on airphotos; but the samples are not distributed by purposive selection.

The landscape unit approach was useful for mapping the plant communities because the boundaries between adjacent landscape units were contiguous; the necessity of extrapolating boundaries between adjacent communities was, therefore, largely precluded. In contrast, extrapolation of boundaries between adjacent communities is necessary when samples are distributed either at random or systematically, and when a boundary is known to lie somewhere between adjacent but spatially isolated samples; in this case all boundaries would have to be determined by field inspection. Determination of community boundaries by use of the landscape unit approach seemed no less accurate than determination by field inspection in Umfolozi Game Reserve.

Extrapolation of community boundaries seems quite simple when inter-sample distances are small, but a large number of samples are required over an area if inter-sample distances are to be kept small. Extrapolation of boundaries was apparently not a problem when Grunow (1967) mapped the vegetation in 1,838 ha of Transvaal Bushveld; Grunow (1967, p 692) considered that 1,238 samples systematically spaced 120 x 120m apart on grid axes were suitable for sampling the woody vegetation. A similar density and spacing of samples would have been impractical for use over the larger 49,280 ha area of Umfolozi Game Reserve. The landscape unit approach seems more practical than a random or systematic distribution of samples if a large area is to be adequately sampled for mapping purposes.

In some respects the landscape unit approach is similar to Küchler's comprehensive method when areas of physiognomically homogeneous vegetation are delineated for mapping purposes (Küchler, 1967 pp 266-276). A main difference being that only vegetation features, and not including other landscape features as used in the landscape unit approach, are used for delineation by Küchler's method. Neither Küchler's (1967) otherwise most comprehensive publication nor any other literature examined deals adequately, if at all, with the ways in which the vegetation of large areas, such as the Reserve, can be studied through use of statistical, phytosociological methods. The landscape unit approach demonstrated in this study of the Reserve could be a small contribution towards the application of such methods to large areas.

6.4.1.2. Sample size and experimental error

An experimental error leading to the misclassification of some samples may have arisen through the choice of six, and not of some other number, point-centred quarters to obtain a sample of the vegetation in a landscape unit. The number of six point-centered quarters was chosen as being the minimal, suitable size of a sample after examination of the species-point (equivalent to species-area) data given in Table 7. But Greig-Smith (1964, p 156) states that there is no necessary relationship between a suitable sample size and minimal area.

Opinion differs widely as to how an unbiased sample size can be determined. Lambert and Dale (1964, p 68) suggest that such a sample size can be determined only after the inter-relationships and distribution of the species are already known; they therefore prefer to fix an arbitrary sample size rather than to determine a suitable sample size by use of species-area curves, as is demonstrated by Cain and Castro (1959, pp 108, 165). An opposite view is expressed by Ivimey-Cook and Proctor (1966, p 190) who recommend a common sense choice of sample size for the sampling of a wide range of vegetation types; they consider that moderate variation in quadrat size will not greatly affect the general features of the results. Purposeful selection of sample size in this manner (not generally favoured by biometricians) may have been useful for different physiognomic types in the Reserve, but was avoided because equal information content was preferred from all samples irrespective of plant density.

The more abundant species in a landscape unit of the Reserve had a better chance of being included in a sample of six point-centered quarters than did the rarer and less abundant species. The findings of Webb, Tracey, Williams and Lance (1967) suggest that the exclusion of the less abundant species from the samples, and from the analysis, would not have detracted significantly from the accuracy of the vegetation classification. Even so, a sample size consisting of a round number of ten point-centers would, in retrospect, have been a better common sense choice than the six point-centers elected. Students of the Wisconsin School sometimes use as many as forty point-centered quarters to estimate plant density (Dr. D. Rogers, pers. com.); such a large number of points was considered unnecessary in the Reserve because the much cruder, qualitative vegetation characteristic of presence was sought.

The low levels of floristic homogeneity discussed in Chapter 6.2.1.2. suggest that the particular position where a sample was located within a landscape unit may have been of critical importance. Six point-centered quarters taken in one part of a landscape unit may have excluded some typical species of the community present in other parts of the landscape unit, and may have included atypical species not found elsewhere in the landscape unit.

This happened in some 43, or less than ten percent, of the landscape units and necessitated a reclassification of their vegetation by field inspection as described in Chapter 3.3.4. Such errors would have been somewhat reduced by the common sense choice of ten or more point-centered quarters; and greater accuracy would have been achieved by placing more than one sample in each landscape unit. The levels of accuracy obtained by the single sample used were regarded as being adequate for the purposes of this study. The majority of the samples included the dominant species upon which the classification of a community depended.

6.4.1.3. Vegetation measures and analysis

The characteristic species listed for each community in Table 31 appeared but once in the Table, and then only for that particular community of which they were characteristic. Braun-Blanquet (1932) did not assign fidelity values for the five degrees of fidelity, so the fidelity values awarded by the author in Chapter 3.3.5. seem, therefore, to be appropriate for vegetation in the Reserve.

The majority of the characteristic species were rare. In just five out of the nine communities were the dominants included amongst the characteristic species, and in two of these five cases the dominants barely achieved characteristic status. The only exclusive species encountered was characteristic of the Riverine Woodland which, in any case, was easily recognisable on a physiognomic basis. The measure of species fidelity was thus generally not very useful for ecological description and field identification of the communities.

On the other hand, the measure of species constancy was much more useful because the most constant species of a community was also the dominant, and it was more easy to environmentally relate the varying degrees of presence seen in a species from community to community.

The main floristic differences between communities in the Reserve were seen to lie in variation of the degrees of presence of the same few species rather than in the absolute presence or absolute absence of a single species. This observation lends more support to the view of Greig-Smith

(1964, p 160) that "the important difference between stands lies in the amount of different species" (i.e. quantitative differences); and lends less support to the view of Lambert and Dale (1964, p 69) that qualitative differences (i.e. absolute presence and absence differences) "may easily override the quantitative element in information-content".

A root cause of the misclassification of some samples in the Reserve by normal analysis (see Chapter 3.3.4.) was that the qualitative, presence and absence records obtained for each sample gave equal weight to all species listed, irrespective of their abundance, whether plentiful or scarce, or other importance. Although the results of normal analysis did provide quantitative values for the overall presence of the species constituting each community, a second field inspection was needed to determine the abundance of species in some misclassified samples in order that the samples could be correctly classified. Purely qualitative records were, therefore insufficient for accurate vegetation classification in the Reserve; and some quantitative data, even if only visually estimated, were needed to supplement the qualitative sample records.

In the above circumstances an ordination technique, which depends on quantitative sample data, and which treats plant communities as part of a vegetation continuum (see McIntosh, 1967), may have been a better way for vegetation analysis in the Reserve rather than the classification technique of normal analysis actually used. Normal analysis depended on qualitative sample records and treated the communities as though they were entirely discrete. But the communities were in fact related as the several parts of one plant formation having overall properties determined by climatic conditions, and all being successional influenced to a greater or lesser extent by fire and edaphic factors. Floristic similarities between the communities of an association prevailed over floristic dissimilarities, and a considerable floristic overlap was detected between the Open, Closed and Riverine Woodland Associations.

The use of an ordination technique for vegetation analysis was discouraged not only because of the great labour involved, but also because of the difficulty in obtaining a

reliable estimate of the absolute measure required of the vegetation. The attempt at estimating density (Chapter 3.1.1.) was abandoned when the sample results were found to differ greatly from a direct count of all trees in the stand. The average values obtained by the point-centered method for inter-tree distance seemed unrealistic of the wide variation in tree density in Open Woodland. Finding a "homogeneous" stand for sampling purposes is more difficult in the Reserve than it evidently would be in Wisconsin. The difficulty of obtaining reliable density data is demonstrated by Lyon (1968) who tested a variety of statistical methods, including some based on plotless and on quadrat techniques, in a community of known density. Lyon (1968) found that many methods would not produce a correct answer with any size of sample, and that all methods required an unreasonably large sample for producing acceptably precise results; he concluded that visual estimates gave more profitable results than did the statistical methods.

6.4.2. Ground layer

6.4.2.1. Physical features

The values summarised in Table 9 for grass height and cover, for forb cover and grazing pressure, are the combined means for the several plots constituting each community. A mean value comprises therefore a fairly wide range of values from within each community. Measurements of grass height and grass cover are variable because of a dependence on both climatic conditions and on the extent to which the grasses were grazed during the season prior to sampling. The values in Table 9 are, therefore, merely relative between the communities as they existed specifically at the time of sampling during March, 1969, and are not absolute values. A discrepancy is thus expected between the text descriptions, based on measurements made during the time of peak growth in March, and the grass features illustrated by some photographs taken at different seasons and in other years.

The assessments of grazing pressure were based on a highly subjective method. A fairly good correlation between grazing pressure and forb cover is visible in Fig. 8.

Future estimates of grazing pressure in the Reserve might thus more profitably be done through a measurement of forb cover, which is more easily and accurately done than the subjectively based assessments.

6.4.2.2. Sampling and analysis

The small number of 350 plots used for sampling the grasses seemed adequate because the plots were distributed amongst the Grassland and all the Woodland Associations such that the ground layer from each woody community was represented. Such a stratified distribution was believed to encompass a wide range of the environmental conditions of the biotic and of the fire influents likely to be experienced by grasses in the Reserve.

The misclassification of some unknown quantity of plots, perhaps to the order of ten percent, during normal analysis was a possibility. The misclassification would have been due to the use of the species presence and absence records, as was the case with the woody plant analysis, and could only have been avoided through use of some other less easily recorded, quantitative vegetation measure. The amount of labour that would have been required for checking all grass plots in the field for their correct classification would likely not have been justified for the small increases expected in accuracy. Besides, it would have been difficult to find the exact category to which belonged some of the plots on clay soil because the communities there represented were as the nodes on a continuous, retrogressive sequence. The grass classification was therefore most safely left in the same form, without amendment, as shown at the short division level in Fig. 4.

Observer error is probably also responsible for some inaccuracy. An occasional, one or two species might well have escaped notice in some plots, particularly if the species were represented by only one or a few individual plants, and even more so if the few plants were heavily grazed almost down to ground level.

6.5. Conclusions

- a. The nature of the Deciduous Acacia Woodland

Formation, and of its fire-maintained sub-climax of Grassland, is determined by the almost arid climate which shows a high moisture deficiency in winter. The moisture deficiency prevails even on comparatively mesic, south aspects and prevents the Woodland from developing into Forest. Succulent communities are found on the driest of north aspects.

b. The distribution of the Themeda Grassland together with the Acacia-Combretum Open Woodland Association corresponds closely with the eluviated Upland Soil Association; the Acacia Spirostachys Closed Woodland Association is mostly found on the illuviated Bottomland Soil Association; and the Acacia-Ficus Riverine Woodland is confined to the perennially moist Riverine Soil Association.

c. A high fertility of the bottomland soils is the main reason why herbivores exhibit a strong preference for grazing the grasses on bottomlands; far smaller quantities of grass are grazed from the less fertile upland soils.

d. Persistent grazing on the bottomlands has denied the resting periods essential for maintaining grass vigour in regions of low, about 600 mm, annual rainfall as found in the Reserve. High grazing pressures exerted by a steadily increasing herbivorous population have severely depleted grass cover in the bottomlands through removing almost the entire annual grass production in places which are not protected from grazing. Persistent grazing and overgrazing have brought the grass communities growing in the bottomlands into a retrograde condition.

e. The grass retrogression proceeds as tall, climax grass species are gradually replaced by shorter, mid-seral and pioneer species more tolerant of frequent defoliation.

f. The advanced stages of the grass retrogression are accompanied by an elimination of fire and of Themeda triandra, by a proliferation of forbs, by encroachment of secondary Thicket, and by accelerated soil erosion.

g. An abundance of autumnal aspect forbs in the poorly grassed bottomlands reflects the infrequency or absence of fire. A scarcity of vernal aspect forbs on the well grassed uplands suggests that burning here has not been

sufficiently frequent to reduce grass competition in spring and so allow a prolific forb growth.

h. The ability of the bottomland grasses to supply adequate fodder during a prolonged drought is questionable unless the retrogression can be checked.

i. The retrogression can be checked through reducing the numbers of grazing animals to a point where they remove much less than one half of the annual bottomland grass production, to the extent that fires can be re-introduced on about a five year cycle.

j. Nearly all woody species in the Reserve, including Thicket forming species, can invade the ground layer provided there is sufficient protection from fire during the early stages of growth.

k. Differences in tree density from one locality to the next are largely governed by the incidence of fire; soil fertility is of lesser importance except that much secondary Thicket encroachment of the bottomlands has come about through the influence of fertility on selective grazing. Soil depth has very little effect on tree density.

l. Soil moisture, the main environmental regulator of tree size, limits tree size in most places excepting on the perennially moist riverine soils, where the largest trees in the Reserve are found.

m. Most of the woody species can, by virtue of their wide ecological amplitude and fire-protective bark, haphazardly succeed in nearly all of the different kinds of habitat in the Reserve.

n. The haphazard manner of succession results in the production of communities in which levels of floristic homogeneity are very low, and which share many floristic similarities. The various communities are not, therefore, always easily recognised in the field. The low levels of homogeneity were revealed when frequency distribution in the Reserve was found not to follow Raunkiaer's Law.

o. The main differences between the communities usually lie in somewhat small differences in the presence of the same few species from one community to the next.

p. The most constantly present species in a community is also the single dominant. The species which becomes dominant in a community is that species which is successional most favoured by the particular soil series or rock type present in the habitat. In addition, micro-climate limits the extent of communities dominated by either Acacia caffra or A. nigrescens.

q. The pattern of community distribution is so closely related to the distribution of soils and of topography that part of a vegetation-soil catena may well be represented in the Reserve.

r. Only 25 out of the 109 species recorded achieve a fidelity of characteristic status. The characteristic species depend for their success on the particular environmental conditions offered by the habitat they occupy; but they are mostly rather rare species, and are not generally useful for field identification of the communities. The greatest proportion of characteristic species is found in the densely wooded Spirostachys africana Closed Woodland where competition between woody plants is exceptionally high compared with other communities. The remaining 84 of the 109 species have such wide ecological amplitudes that they can establish in nearly all of the habitats presented in the Reserve.

s. The landscape unit approach was useful for indicating what number of samples might be adequate for sampling the vegetation of the Reserve, and for suggesting where they might profitably be distributed. Some bias could, however, have been introduced through use of this approach. Distribution of the comparatively few 531 samples by the landscape unit approach seemed an efficient way for obtaining vegetation samples from the comparatively large 49,280 ha area of the Reserve. The approach was also a useful aid for mapping purposes as the need for extrapolation of community boundaries in the field was mostly precluded.

t. The use of species presence-and-absence records alone seems inadequate for characterisation of some samples; if misclassification is to be rectified some quantitative information, such as abundance or density, should also be

recorded for the samples.

u. Practical difficulties mitigated against the dependence of quantitative records for characterisation of the samples, and thereby precluded the use of an ordination technique which might have been better for analysis of the vegetation than was the classification technique actually used.

v. The Reserve is included amongst the few, least disturbed areas of Deciduous Acacia Woodland remaining in Natal; and it still retains a good proportion of its original complement of wild animal species. A wide range of landforms, including hills, scarps, valleys and alluvial terraces, and a variety of soils together with a wealth of plant life constitute the landscape of the Reserve. The Reserve provided a unique opportunity for studying the succession and ecology of plant communities in relation to their habitats and the biota. The Reserve therefore warrants preservation on scientific grounds quite apart from other important aesthetic, recreational and conservation reasons.

* * * * *

CHAPTER SEVEN

MANAGEMENT RECOMMENDATIONS

7.1. Introduction

The management recommendations offered from this study are confined to considerations of veld management. Other subjects excluded from the present terms of reference, such as usage policy and tourist recreation, as well as the results of more recent research will also need consideration when a full management plan is drafted for the Reserve.

The key to conservation of the vegetation, the animals and their habitats lies in correct management of the grass communities. The management would depend almost entirely on the control of herbivore numbers and on the wise usage of fire because rotational grazing systems, which allow for the resting, burning and recovery of grasses, require internal fences: division of the Reserve into a number of camps through fencing is not practicable.

Some of the most denuded areas could, however, be protected through use of barriers other than fences, such as strips of plastic sheeting or brushwood. Herbivores are reluctant to cross unfamiliar, one metre wide sheets of opaque plastic placed on the ground. Some eroded areas in the Hluhluwe Game Reserve have been successfully protected from trampling and rested from grazing by a dense layer of brushwood packed over the soil; but only small areas of a few hectares or so can thus be protected because of the large amount of labour required and, sometimes, because insufficient supplies of suitable brushwood are close at hand (Mr. R. Porter, pers. com.).

For practical purposes of management the Reserve is divisible into two major parts, the uplands and the bottomlands, which have different problems and which require separate treatments.

7.2. Upland management

The uplands comprise approximately 246 km², or one half of the total area of the Reserve. The uplands take in the entire extent of the Miocene Surface as well as the

hill tops, ridges and steep hill sides of the Pliocene Surface.

Management of the uplands will be a simple matter because the small amounts of grass here removed, estimated at 148 kg/ha/yr in Chapter 5.1.2.2.2., leave a surplus of grass more than sufficient to allow for resting of the veld and for grass seeding. There is little chance during the next five years of the uplands becoming over-grazed unless exceptionally large increases take place in the numbers of buffalo and zebra, the principal grazers of uplands. The main questions to be decided on the upland management concern the season of burning and the duration of the intervals between successive burns. The solution of these questions is apparently not a matter of priority as present management practices are satisfactory for purposes of soil conservation.

A good season for burning seems to be during the first week of August. This is rather early, but the green flush of grass which would follow, particularly in the event of early rains, might help draw numbers of herbivores away from the bottomlands which would thereby benefit from some rest during the early stages of grass regrowth. An early burn of the uplands would also benefit the beautiful vernal aspect forbs.

The interval chosen for separating successive burns will mostly depend on the desired extent of invasion of the uplands by woody plants. Many of the woody invaders, notably Acacia spp., are useful browse plants and so numbers can be encouraged, but not to the extent that Thicket development is permitted. The browse plants are most useful when their crowns are kept close, within about three metres, to the ground and are within reach of the majority of browsing herbivore species. A young growth of soft twigs is better browsing material than an older growth of highly fibrous branches. A three year interval between burns would seem to satisfy the preceding desiderata for the uplands.

Some additional information gained from current and future research on the food requirements and preferences of browsers may well indicate that some other season or interval is better for burning. Management of the uplands for optimal browse productivity will, however, also depend

on acquiring detailed information on the circumstances surrounding the seed production, dispersal and germination of the preferred browse plants as well as the reaction of their saplings to different seasons and frequencies of burning. The same applies for browse productivity in the bottomlands where, in addition, the propagation of undesirable Thicket forming species could profitably be studied.

Approximately one-third of the uplands, corresponding with the recommended burning interval of three years, could be burned each year. The various areas to be burned in any one year should be as widely distributed as possible. The distribution of the areas is facilitated if the Miocene hills and associated Pliocene ridges are grouped into the following nine regions. One or more of the upland areas constituting each region can be burned annually so that a three year rotational burn is achieved in each region. A convenient choice of the boundaries of an area to be burned will depend at the time of burning on practical considerations of wind direction, and of places where the fire can be easily checked, whether along a rock outcrop, a stream, an overgrazed bottomland, a road or a previously burned firebreak. Firebreaks are normally burned early in winter as soon as the grass is sufficiently dry; the early burning of firebreaks is a precaution against uncontrolled, accidental fires.

The nine regions comprising the upland areas are proposed as follows.

1. Mzaneni, Khukho, Ntoyiana.
2. Sokhwezele, Zintuntzini, Ntabayamanina, Sabokwe.
3. Lubisana, Mhlolokazana, Nqolothi.
4. Tobothi, Mbhuzane, Mbulunga, Msasaneni.
5. The Madlozi-Chibilethangwe ridges, Mantiyane.
6. Mpila encane, Matshemnyama (north), Mpila, Shoshangesisila.
7. Dengezi, Matshemnyama (east), Matshemhlophe.
8. Tshenteka, Chibilenyathi, Tshenilentombi, Luthelezi-Ncoki, Mduba.
9. Makhamisa, Qaqalwempisi, Ciyana, Ngceba.

7.3. Bottomland management

The bottomlands take in the entire extent of the

Quaternary Surface, which can be regarded as all the country lying below the 600 ft (180m) contour, as well as the lower parts of the Pliocene Surface occupied by the valleys of the Thobothi, Gqoyini and Mphafa Streams. The bottomlands take in about 246 km² or one half of the extent of the Reserve.

The first priority of bottomland management should be to check the grass community retrogression and so allow the restoration of an ideal grass cover. An ideal grass cover would generally show the following properties, depending on the amount of rainfall received, at the season of peak growth normally in March or April:

- (a) a grass height of greater than 50 cm;
- (b) a grass cover of greater than 40 percent;
- (c) a forb cover of ten percent or less;
- (d) abundant plants of Themeda triandra;
- (e) few or no plants of unpalatable species of Bothriochloa, of Cymbopogon and of Aristida.

Themeda triandra is a most useful indicator plant in the Reserve. Wherever T. triandra is abundant the veld is nearly always in a healthy condition; a scarcity or extensive absence of T. triandra indicates a poor veld.

The only way in which the ideal grass cover could be restored is through controlling the numbers of herbivores which use the bottomlands. Over-utilisation of the bottomlands will likely give rise to a perennial management problem because the herbivores, no matter how few in number, will always tend to concentrate on their preferred grazing grounds in the bottomlands where the most fertile soils and the most palatable grasses are to be found. One or both of the following steps could be taken towards reducing the severity of the management problem.

(i) The herbivore numbers could be reduced to such an extent that the remaining herbivores are incapable of removing more than 50 percent of the available, annual grass growth in the bottomlands.

(ii) The bottomlands could be divided off into about five areas, based on the catchments of the major streams, which could receive a rotational fire treatment such that no more than one-fifth of the total extent of the bottomlands is burned in any one year, and such that each one of the areas

is burned on a five year cycle.

The area or catchment selected for burning should be protected, as far as is reasonably possible, from grazing for the 12 month period before it is fired in August or September. The protection is required so that litter sufficient for burning can accumulate. The protection could be achieved in the following ways.

1. Nearly all game control, whether done by capture or culling, for the year should be done in the selected catchment. If more animals are required for game control purposes than are available from the selected catchment, then the shortfall could beneficially be obtained from adjacent catchments. Apart from the bodily removal of the game, some extra degree of veld protection would accrue from the disturbance caused by the control activities. The disturbance would partly discourage a movement into the catchment of animals from elsewhere.

2. Any watering places in the catchment should, where possible, be fenced off (either by use of wire, brushwood, or opaque plastic sheeting) after game control operations have been completed so that any residual animals are encouraged to move out and drink elsewhere. This would not normally be a difficult task as few watering places persist in the catchments during the dry season. The effects which such a measure may have on the territorial or other social behaviour of certain animals have not been taken into account.

3. The use of brushwood or opaque plastic sheeting could be contemplated, if economically possible, for protecting the most denuded parts of some catchments.

4. Some herbivores could be drawn away from the protected catchment to nearby upland areas where an attractive flush of new grass might be induced by an early burn as mentioned in Chapter 7.2.

The second priority of bottomland management should be to combat any further extension in the areas of secondary Thicket. Further increases in the present extent of secondary Thicket should be discouraged because the Thickets reduce the valuable areas of available grazing, and

because many of the woody invaders which form the Thickets are not very useful species for browsing purposes.

A possible use of herbicide for Thicket control in the Reserve is felt to be unjustifiable because proper burning management will do the job more cheaply. The introduction of herbicide, which is an element foreign to the landscape, is regarded as undesirable in a nature reserve because toxic residues could have a harmful effect on soil micro-organisms.

The re-introduction of fire as a tool for Thicket control in the bottomlands will be possible only after the first priority, the restoration of an ideal grass cover, has been successfully achieved - as will be shown when the grasses are sufficiently dense to permit burning at the end of winter. The indigenous grasses are remarkably quick to recover provided that an adequate degree of protection is given from grazing and trampling, and provided that adequate rainfall is received. Panicum maximum, which is not strictly a pioneer grass but which is a prolific seeder, was found to have densely colonised denuded areas in the Reserve within about three years after the areas were protected by brushwood. The re-introduction of fire to the bottomlands might, therefore, be possible within from three to five years after an adequately large number of grazing animals have been removed.

A desirable frequency for burning of the bottomlands can be determined, either by experimentation or observation, only after the grasses have been restored to the ideal condition. An interval of about five years between successive burns may turn out to be suitable because a certain number of woody invaders, particularly those which are useful browse and shelter plants, should be encouraged. Themeda triandra may well become a common plant of the bottomlands after one or several cycles of fire have passed through the bottomlands, but its abundance here will not be of paramount importance provided an ideal, 40 percent or more, cover is established of other grasses, including such as the shade tolerant plants of Panicum maximum, P. deustum and the other species which are also favourite food plants.

The time of burning should be left over as late

as possible before the first rains of summer so that as much pasturage as possible, albeit in the form of dead litter, is available to the herbivores until the rains ensure a supply of fresh growth. The advent of the first summer rains cannot be precisely predicted, but burning could in most years be safely delayed until about the end of August or beginning of September. Burning should be completed before the end of September because of the good rains expected in October. Current opinion is that recent growth should not be burned when the grasses are in a fairly green condition as a result of good rains.

Thicket control should not be attempted until after the number of herbivores has been reduced. A number of grass plants that survive at present in the shelter of Thicket plants and other woody invaders will assist in the re-colonisation of bare areas by sending out seed. An early removal at the present time of these woody plants, either by fire or by felling, would be most harmful in that the bulk of the surviving grasses would be made immediately available to the herbivores; and the valuable centres of seed production would be lost. Premature timing of Thicket control done before adequate game control or before grass recovery will be wasted effort because woody encroachment will recur either in the absence of grass competition or in the absence of fire. However, Thicket branches cut after the grass recovery would protect the grasses for several seasons from grazing if the branches were left lying on the ground.

A third priority of the bottomland management, the control of soil erosion, is not believed to require direct action at the present moment. The stabilisation of soil-eroded areas by means of mechanical structures is extremely expensive and seems mostly unwarranted at present, excepting in a few cases as, for instance, where a gully is encroaching upon a road. Further erosion along roads can be prevented by placing, and maintaining, adequate road drains. Effective erosion control in the bottomlands will be possible only when the present poor grass cover, which is the main cause of the erosion, has been replaced by the ideal grass cover. It is expected that much of the erosion will have been biologically checked once the number of

herbivores has been sufficiently reduced and the ideal grass cover restored. The use of mechanical structures could be contemplated in the future for those gulleys which may not have been checked by the biological measures. Some of the mechanical structures placed during the last five years in the Khandaledube catchment have, on several occasions, been damaged or swept away because the sparse grass cover was incapable of retarding the swift run-off produced from heavy rain storms.

The conservation measures recommended above for management during the next five years, whether in connection with herbivore control, restoration of grass cover, Thicket or erosion control, are regarded as being practical because no further financial expenditure or additional personnel would be required than are already being used for the running of the Reserve. On the other hand, some alternative possibilities for veld management, such as the use of herbicides, bush clearing or mechanical structures, would entail additional spending and more personnel.

7.4. Herbivore control

The sparsity of grass cover and the extent of grass community retrogression, as well as the easily erodible nature of the soils, in the bottomlands indicates that a moderately large proportion of the herbivores should be removed, preferably by capture and translocation out of the Reserve or, alternatively, by culling. Such control measures are necessary for restoration of the grass cover, for preservation of the habitats, and for the ultimate success of the herbivores.

The aim of control should be to reduce the numbers of herbivores that graze in the bottomlands to an extent that the minimal grass demand of the bottomlands is reduced by more than one half, from the present calculated 678 kg/ha/year to about 300 kg/ha/year. The latter amount would correspond with a 33 percent utilisation of the possible production of 1000 kg/ha/year which the bottomlands are expected to produce once they have been sufficiently protected and are allowed to develop the ideal, healthy grass cover. The 33 percent utilisation is just within

the maximum permissible suggested for healthy Acacia Woodland where a removal of more than 40 or 50 percent of the annual grass production can cause veld damage (West, 1955, p 628).

The reduced level of the herbivore population which uses about 300 kg/ha/year of the bottomland grasses can be termed the recovery level. Such large numbers of herbivores will have to be removed to reach the recovery level that several years may be needed to effect control, but the recovery population should preferably be achieved by August, 1975, at the latest.

Decisions as to the exact numbers, sex ratios and age-class proportions of the various herbivores to be removed lie beyond the scope of a plant ecologist; but these subjects are open for discussion during meetings held by personnel of the Natal Parks Board who represent a wide range of disciplines. The following general suggestions are, however, offered with reference to Table 30.

(a) No control measures should be taken against the smaller and rarer herbivores, such as reedbuck, mountain reedbuck, bushbuck, and steenbok; neither against the purely browsing species such as kudu, unless the kudu is thought to be over-competing for browse against the bushbuck, which is believed to be on the decrease.

(b) Little or no control is needed of buffalo and zebra as they are mainly upland grazers.

(c) Warthog and waterbuck should be kept at about their present levels through removal of numbers equivalent to their annual increments. A reduction in the number of waterbuck to 500 would benefit the heavily utilised bottomland areas, but an over-reduction should be avoided if possible because the Reserve is the waterbuck's main stronghold in Natal.

(d) Large reductions, to the order of 70 percent, could be applied to nyala and impala which make heavy use of the bottomlands. These animals are well represented outside the Reserve which, in any case, was only recently included within their distribution range (see Mentis, 1970). Reductions of 70 percent in impala and nyala would save a total of 470 tonnes per annum of bottomland grasses.

(e) A reduction of the white rhinoceros population from the present number of 1,336 to 500 animals would save some 7,450 tonnes per annum of bottomland grass production. A lesser reduction of the white rhinoceros would have to be compensated for by such large reductions amongst the other bottomland utilisers that they would be almost eliminated.

(f) A fifty percent reduction of the wildebeest to 700 animals would save some 1,200 tonnes of bottomland grass per annum.

(g) The bottomland grass savings that could be achieved by the reductions suggested at (d), (e) and (f) above would reduce the present estimated total grass demand of 16,670 tonnes per annum by 9,120 tonnes to 7,550 tonnes. The grass savings amount to 46 percent of the total present demand. This is a little under, but almost equal to, the 50 percent reduction recommended for recovery of the bottomland grasses. The herbivore reductions recommended above are therefore close to the minimum to be applied if anything like the ideal grass cover is to be achieved.

(h) The principal bottomland grazers, the white rhinoceros, wildebeest, impala and nyala, will probably have to be kept at the recovery levels suggested above until such time as something like the ideal grass cover is achieved.

* * * * *

A LIST OF ANGIOSPERMS RECORDED IN
UMFOLOZI GAME RESERVE

Angiosperm families and genera are listed in sequence according to the arrangement of Phillips (1951). Species are listed alphabetically.

The list includes most of the angiosperm species recorded in the Reserve. Those species collected by the author are listed together with my collector's number; other species not collected by the author but which have been collected in the Reserve are not accompanied in the list by a collector's number. Herbarium specimens of all species collected in the Reserve are lodged in the Herbarium, Hluhluwe Game Reserve, P.O.Box 25, Mtubatuba, Natal. Duplicate specimens of some species have been sent to the Herbarium at the University of Natal, Pietermaritzburg.

Those species marked on the list by an asterisk were recorded as present in the Reserve but have not been collected. These uncollected species were either already sufficiently well known to the author, or were readily identifiable by reference to such books as Codd (1951) and Ross (1971).

The larger proportion of all tree, shrub and grass species likely to be present in the Reserve is probably included by the list; but forbs are poorly represented.

POTAMOGETONACEAE

Cymodocea ciliata (Forsk.) Ehrenb. ex Aschers.

GRAMINEAE

<u>Imperata cylindrica</u> (L.) Beauv. var. <u>major</u> Nees	..	583
<u>Ischaemum arcuatum</u> (Nees) Stapf	..	542
<u>Hemarthria altissima</u> Stapf & C.E. Hubb.	..	540
* <u>Trachypogon spicatus</u> (L.f.) O.Kuntze		
<u>Elynonurus argenteus</u> Nees	426,	438
<u>Andropogon appendiculatus</u> Nees		
<u>Sorghum halepense</u> (L.) Pers.	..	470
<u>Bothriochloa insculpta</u> (Hochst.) A. Camus	429,	565
<u>Cymbopogon excavatus</u> (Hochst.) Stapf		
<u>Cymbopogon marginatus</u> (Steud.) Stapf	..	567
<u>Cymbopogon plurinodis</u> Stapf	430,	580
<u>Cymbopogon validus</u> Stapf ex Burt Davy		
<u>Hyparrhenia filipendula</u> (Hochst.) Stapf var.		
<u>pilosa</u> (Hack.) Stapf	553,	566
<u>Hyparrhenia hirta</u> (L.) Stapf	..	578
<u>Heteropogon contortus</u> (L.) Beauv.	..	447
<u>Diheteropogon amplexans</u> (Nees) W.D. Clayton	488,	526
<u>Hyperthelia dissoluta</u> (Nees ex Steud.)		
W.D. Clayton	502a,	571
<u>Themeda triandra</u> Forsk. var. <u>trachyspatha</u>		
Goosens	..	428
<u>Tragus berteronianus</u> Schultz	..	444
<u>Perotis patens</u> Gand.	418,	445
<u>Paspalum commersonii</u> Lam.	..	626
<u>Paspalum distichum</u> L.	..	627
<u>Paspalidium</u> sp. Stapf		
<u>Eriochloa borumensis</u> Stapf		
<u>Panicum coloratum</u> L.		
<u>Panicum deustum</u> Thunb.	..	425
<u>Panicum maximum</u> Jacq.	..	471
<u>Panicum meyerianum</u> Nees var. <u>grandiglume</u> Stent		
& Rattray	548,	615
<u>Urochloa mosambicensis</u> (Hack.) Dandy	..	441
<u>Urochloa trichopus</u> (Hochst.) Stapf	..	524
<u>Brachiaria deflexa</u> (Schum.) C.E. Hubb. ex Robyns	..	468
<u>Brachiaria dictyoneura</u> Fig. & de Not.	..	525
<u>Brachiaria eruciformis</u> (Sibth. & Smith) Griseb.	..	520
<u>Brachiaria humidicola</u> (Rendle) Schweick.		
<u>Brachiaria nigropedata</u> (Munro) Stapf	..	434
<u>Brachiaria ramosa</u> Stapf		
* <u>Brachiaria serrata</u> (Sprang.) Stapf		
<u>Brachiaria xantholeuca</u> (Hack.) Stapf		
<u>Echinochloa colonum</u> (L.) Link	551,	581
<u>Echinochloa holubii</u> Stapf		
<u>Sacciolepis curvata</u> (L.) Chase		
<u>Digitaria argyrograptus</u> (Nees) Stapf	..	521
<u>Digitaria debilis</u> Willd.		
<u>Digitaria eriantha</u> Steud.		
<u>Digitaria longiflora</u> (Retz.) Pers.	442,	523
<u>Digitaria macroglossa</u> Henrard	..	501a
<u>Digitaria natalensis</u> Stent		
<u>Digitaria pentzii</u> Stent		

<u>Digitaria polevansii</u> Stent	..	519
<u>Digitaria smutsii</u> Stent	..	467
<u>Tricholaena monachne</u> (Trin.) Stapf & C.E.Hubb.	446, 464,	508
<u>Rhynchelytrum repens</u> (Willd.) Hubbard	..	415
<u>Rhynchelytrum villosum</u> (Parl.) Chiov.	..	582
<u>Setaria perennis</u> Hack.	..	448
<u>Setaria sphacelata</u> (Schum.) Stapf & C.E.Hubb. ex M.B.Moss	..	522
<u>Setaria verticillata</u> (L.) Beauv.	..	564
<u>Setaria woodii</u> Hack.	..	439
<u>Cenchrus ciliaris</u> L.	469,	514
<u>Aristida bipartita</u> (Nees) Trin. & Rupr.	..	511
<u>Aristida congesta</u> Roem. & Schult. ssp. <u>barbicollis</u> (Trin. & Rupr.) de Winter	413, 574,	576
<u>Aristida congesta</u> Roem. & Schult. subsp. <u>congesta</u>	505,	575
<u>Aristida curvata</u> (Nees) Trin. & Rupr.		
<u>Aristida diffusa</u> Trin. var. <u>burkei</u> Schweick.	..	572
<u>Aristida scabrivalvis</u> Hack.		
<u>Aristida stipitata</u> Hack. var. <u>graciliflora</u> (Pilger) de Winter	431,	577
<u>Sporobolus festivus</u> Hochst.		
<u>Sporobolus fimbriatus</u> Nees		
<u>Sporobolus fimbriatus</u> Nees var. <u>latifolia</u> Stent (The glumes resemble those of <u>S. fouriadii</u> Stent.)	..	503a
<u>Sporobolus nitens</u> Stent	..	440
<u>Sporobolus pyramidalis</u> Beauv.	427,	579
<u>Sporobolus smutsii</u> Stent	..	437
<u>Sporobolus stapfianus</u> Gand.	..	420
<u>Sporobolus virginicus</u> (L.) Kunth		
* <u>Tristachya hispida</u> (L.f.) K. Schum.		
<u>Cynodon dactylon</u> (L.) Pers.	..	443
* <u>Harpechloa falx</u> (L.) O. Ktze.		
<u>Enteropogon monostachyos</u> (Vahl) K. Schum. ex Engl. subsp. <u>africanus</u> W.D. Clayton	..	423
<u>Chloris gayana</u> Kunth	..	541
<u>Chloris pycnothrix</u> Trin.	..	539
<u>Chloris virgata</u> Sw.	..	513
<u>Eustachys paspaloides</u> (Vahl) Lanza & Mattei	414,	466
<u>Tripogon abyssinicus</u> Nees		
<u>Tetrapogon mosambicensis</u> (K. Schum.) Chippindall ex B.S. Fisher	..	518
<u>Eleusine indica</u> Gaertn.	..	538
<u>Dactyloctenium australe</u> Steud.	..	509
<u>Dactyloctenium giganteum</u> Fisher & Schweick.	..	515
<u>Leptochloa panicea</u> (Retz.) Ohwi	..	563
<u>Enneapogon cenchroides</u> (Roem. & Schult.) C.E. Hubb.	..	506
<u>Enneapogon scoparius</u> Stapf	..	465
<u>Fingerhuthia africana</u> Lehm.	..	544
* <u>Phragmites australis</u> (Cav.) Trin. ex Steud.		
<u>Phragmites mauritianus</u> Kunth	..	651
<u>Diplachne eleusine</u> Nees	..	433
<u>Diplachne fusca</u> Beauv.		
<u>Pogonarthria squarrosa</u> (Licht.) Pilger	..	504
<u>Trichoneura grandiglumis</u> (Nees) Stapf & Hubb.	..	419
<u>Eragrostis barbinodis</u> Hack.	573,	507
<u>Eragrostis cilianensis</u> (All.) Lutati	512,	547
<u>Eragrostis ciliaris</u> (L.) R. Bse.	569,	628
<u>Eragrostis curvula</u> (Schrad.) Nees	..	416

<u>Eragrostis gummiflua</u> Nees	..	549
<u>Eragrostis heteromera</u> Stapf	..	510
<u>Eragrostis superba</u> Peyr.	..	417

CYPERACEAE

<u>Cyperus articulatus</u> L.	..	629
<u>Cyperus difformis</u> L.	..	562
<u>Cyperus leptocladus</u> Kunth	..	436
<u>Cyperus margariticeus</u> Vahl	..	435
<u>Cyperus maritimus</u> Poir.		
<u>Cyperus obtusiflorus</u> Vahl	..	449
<u>Cyperus rupestris</u> Kunth	450, ..	620
<u>Cyperus sexangularis</u> Nees	..	616
<u>Cyperus teneriffae</u> Poir.	..	421
<u>Cyperus textilis</u> Thunb.		
<u>Juncellus laevigatus</u> C.B. Cl.		
<u>Marisus binucifer</u> C.B. Cl.	..	423
<u>Mariscus inflatus</u> C.B. Cl.		
<u>Mariscus vestitus</u> C.B. Cl.	..	619
<u>Kyllinga erecta</u> Schumach.	..	422
<u>Kyllinga melanosperma</u> Nees		
<u>Scirpus articulatus</u> L.		
<u>Scirpus cernuus</u> Vahl		
<u>Scirpus muricinux</u> C.B. Cl.		
<u>Scirpus paludicola</u> Kunth		
<u>Scirpus praelongatus</u> Poir.		
<u>Fimbristylis hispidula</u> (Vahl) Kunth	..	463
<u>Fimbristylis monostachya</u> (L.) Hassk.		
<u>Bulbostylis boeckleriana</u> (Schweinf.) K.D.H.	..	424

PALMAE

- * Phoenix reclinata Jacq.
- * Hyphaene crinita Gaertn.

COMMELINACEAE

<u>Commelina africana</u> L.	..	533
<u>Commelina benghalensis</u> L.	..	536
<u>Murdannia simplex</u> (Vahl) Brenan	..	617

JUNCACEAE

Juncus lomatophyllus Spreng.

LILIACEAE

<u>Bulbine natalensis</u> Bak.		
<u>Anthericum galpinii</u> Bak.	..	600
<u>Eriospermum burchellii</u> Bak.		
<u>Eriospermum galpinii</u> Schinz		

- * Aloe marlothii Berger
 * Aloe vanbalenii Pillans
Gasteria sp. Duval
Albucca pachychlamys Bak.
Dipcadi gracillimum Bak.
Scilla sp. L. .. 604
Ornithogalum ecklonii Schltr.
Asparagus falcatus L.
Asparagus macowanii Bak. var. zuluensis (N.E.Br.)
 Jessop
Asparagus subulatus Thunb.
Asparagus virgatus Bak. .. 550

AMARYLLIDACEAE

- Haemanthus multiflorus Martyn
Ammocharis coranica Herb.
 * Ammocharis falcata Herb.
Cyrtanthus galpinii Bak.

IRIDACEAE

- Lapeyrouisia laxa (Thunb.) N.G.Br.

MUSACEAE

- Strelitzia regina Ait.

SALICACEAE

- Salix woodii Seeman

ULMACEAE

- * Chaetacme aristata Planch.

MORACEAE

- Ficus capensis Thunb.
 * Ficus capreaefolia Del.
Ficus pretoriae Burt Davy .. 596
 * Ficus soldanella Warb.

<u>Ficus benderi</u> Miq.	..	589
<u>Ficus stuhlmanii</u> Warb.	..	487
<u>Ficus sycamorus</u> L.	..	595

URTICACEAE

Urera tenax N.E.Br.

LORANTHACEAE

Loranthus kraussianus Meisn.
Loranthus natalitius Meisn.
Loranthus ngamius Sprague

SANTALACEAE

Thesium resedoides A.W.Hill

OLACACEAE

Ximenia caffra Sond.

POLYGONACEAE

Polygonum salicifolium Brouss.

CHENOPODIACEAE

Chenopodium album L. .. 558

AMARANTACEAE

Achyroopsis leptostachya Hook. f.
Cyphocarpa angustifolia Lopr. .. 529
Cyathula spathulifolia Lopr.
Alternanthera repens (L.) O.Kuntze
Gomphrena celosiodes Mart. .. 601

NYCTAGINACEAE

Boerhaavia diffusa L.

AIZOACEAE

- Hypertelis salsoloides (Burch.) Adamson
 * Aizoon canariense L. .. 543
Aizoon glinoides L.f. .. 537
Aptenia cordifolia (Lf.) N.E.Br.
Delosperma pachyrrhizum L.Bol.

PORTULACACEAE

- * Portulacaria afra Jacq. .. 537b
Portulaca kermesina N.E.Br. .. 610
Portulaca quadrifida L.

CARYOPHYLLACEAE

Dianthus zeyheri Sond. subsp. natalensis Hooper

CERATOPHYLLACEAE

Ceratophyllum demersum L.

MENISPERMACEAE

Cissampelos mucronata A.Rich.

CAPPARIDACEAE

- Cleome diandra Burch.
Cleome monophylla L.
Capparis tomentosa Lam.
 * Boscia albitrunca (Burch.) Gilg. & Bened. .. 649
Maerua angolensis DC.
Maerua rosmarinoides (Gand.) Gilg. & Ben.

CRASSULACEAE

Crassula argentea Thunb.
Crassula transvaalensis (O.K.) K.Schum.

LEGUMINOSAE

- Acacia borleae Burt Davy. .. 481
Acacia brevispica Harms var. schweinfurthii
 (Brenan and Exell) Ross and Gordon-Gray .. 561
Acacia burkei Benth. 250a, 585
 Most specimens in the Reserve are hybrids
 between A. burkei and A. nigrescens (Dr J. Ross,
 pers.comm.)
Acacia caffra (Thunb) Willd.
Acacia gerrardii Benth.
Acacia grandicornuta Gerstnr.
Acacia karroo Hayne 482, 451
Acacia luederitzii Engl. var. retinens (Sim)
 Ross & Brenan
Acacia nigrescens Oliv.
 * Acacia nilotica (L.) Del.
Acacia robusta Burch. subsp. clavigera (E.Mey.)
 Brenan
 * Acacia senegal (L.) Willd.
Acacia sieberiana DC. var. woodii (Burt Davy) .. 552
 Key & Brenan
 Very rare in Reserve, known only from
 Makhamisa area.
 * Acacia tortilis (Forsk.) Hayne
 * Dichrostachys cinerea (L.) Wight & Arn.
Entada wahlbergii Harv. .. 597
Schotia brachypetala Sond.
Schotia capitata Bolle .. 479
Peltophorum africanum Sond.
Crotalaria monteiroi Taub. ex Bak.
Indigofera costata Guill. & Perr.
Indigofera sp. N.E.Br. (= K.Tinley no.850) .. 614
Mundulea sericea (Willd.) A.Chev.
Sesbania bispinosa (Jacq.) F.W.Wr.
 * Ormocarpum trichocarpum (Taub.) Engl.
Stylosanthes fruticosa (Retz.) Mohl.
Glycine wightii (R.Grah. ex Wight & Arn.) Verdcourt
Erythrina sp. L. .. 592
Rhynchosia nitens Benth.
Vigna longiloba Burt Davey .. 605

OXALIDACEAE

Oxalis smithii Eckl. & Zeyh.

ERYTHROXYLACEAE

Erythroxylum delagoense Schinz .. 587

ZYGOPHYLLACEAE

Tribulus terrestris L. .. 534
Balanites maughamii Sprague

RUTACEAE

Fagara capensis Thunb.

BURSERACEAE

* Commiphora harveyi Engl. .. 458
Commiphora neglecta Verdoorn
Commiphora pyracanthoides Engl.
Commiphora schimperi (Berg.) Engl.

MELIACEAE

Turraea obtusifolia Hochst. .. 586
 * Trichilia emetica Vahl

MALPIGHIACEAE

Sphedamnocarpus galphimifolius (A.Juss.) Szyszyl.

POLYGALACEAE

Polygala serpentaria Eckl. & Zeyh. .. 599

EUPHORBACEAE

Securinega virosa (Roxb. ex Willd.) Pax & Hoffm. 517
Phyllanthus maderaspatensis L. .. 603
Croton menyhartii Pax .. 477
Erythrococca natalensis Prain

<u>Acalypha glabrata</u> Thunb.	
<u>Acalypha indica</u> L.	.. 557
<u>Trupla meyeriana</u> Muell. Arg.	
<u>Jatropha variifolia</u> Pax	
* <u>Spirostachys africana</u> Sond.	
* <u>Euphorbia grandicornis</u> Goebel	
<u>Euphorbia matabelensis</u> Pax	
* <u>Euphorbia tirucalli</u> L.	

ANACARDIACEAE

<u>Sclerocarya caffra</u> Sond.	
<u>Ozoroa engleri</u> R.& A. Fernandes	.. 591
<u>Ozoroa obovata</u> (Oliv.) R.& A. Fernandes	.. 460
<u>Ozoroa paniculosa</u> (Sond.) R.& A. Fernandes	.. 640
<u>Rhus chirindensis</u> Bak.f.	.. 584
<u>Rhus gueenzii</u> Sond.	
<u>Rhus pentheri</u> A. Zahlbr.	.. 461
<u>Rhus simii</u> Schonl.	.. 480

CELASTRACEAE

<u>Maytenus heterophylla</u> (Eckl. et Zeyhr.) N. Robson	478
<u>Maytenus senegalensis</u> (Lamb) Exell.	
(Some plants recorded in Closed Woodland areas of the Reserve correspond with <u>M. cymosus</u> forma DE 1253 described by Edwards, 1967, p 269).	
<u>Maytenus undatus</u> (Thunb.) Blakelock.	
<u>Cassine aethiopica</u> Thunb.	.. 474
<u>Cassine papillosa</u> Kuntze	
<u>Pseudocassine transvaalensis</u> (Burt Davy) Bredell.	457

ICACINACEAE

Pyrenacantha grandiflora Baill.

SAPINDACEAE

- Deinbollia oblongifolia (Arn.) Radlk.
- * Pappea capensis Eckl. & Zehy.
- Hippobromus pauciflorus (L.f.) Radlk.

RHAMNACEAE

Ziziphus mucronata Willd.

Phyllogeiton zeyheri (Sond.) Suesseng.

VITACEAE

<u>Rhoicissus digitata</u> Guth.& Bol.		
<u>Rhoicissus tomentosa</u> (Lam.) Wild & Drummond	..	593
* <u>Cissus quadrangularis</u> L.		
<u>Cissus rotundifolia</u> Vahl	..	624
<u>Cyphostemma schlechteri</u> (Gilg et Brandt) Desc.	..	623

TILIACEAE

<u>Grewia bicolor</u> Juss.		
<u>Grewia caffra</u> Meisn.	..	473
<u>Grewia flava</u> DC.	..	608
<u>Grewia flavescens</u> Juss.		
* <u>Grewia hexamita</u> Burret		
<u>Grewia monticola</u> Sond.	..	639
<u>Grewia occidentalis</u> L.	..	609
<u>Grewia</u> sp. cf. <u>G. kwebensis</u> N.E.Br.		
<u>Grewia subspathulata</u> N.E.Br.		
<u>Grewia villosa</u> Willd.	..	494

MALVACEAE

<u>Abutilon austro-africanum</u> Hochr.		
<u>Abutilon</u> sp. Under revision.	..	535
<u>Hibiscus pusillus</u> Thunb.	..	632
<u>Thespesia acutiloba</u> (Bak.f.) Exell & Mendonca	..	456
<u>Cienfuegosia hildebrandtii</u> Gatke	..	631
<u>Gossypium transvaalense</u> Watt	..	546

STERCULIACEAE

<u>Melhania didyma</u> Eckl.& Zeyh.		
<u>Dombeya cymosa</u> Harv.	..	475
<u>Dombeya rotundifolia</u> Planch.		
<u>Waltheria indica</u> L.		

OCHNACEAE

<u>Ochna natalitia</u> Engl.& Gilg.	..	545
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GUTTIFERAE

FLACOURTIACEAE

- * Scolopia zeyheri (Nees) Szyszyl.

CACTACEAE

Rhipsalis baccifera (J.Mill.) Stearn

THYMELACEAE

Lasiosiphon splendens Engl.

.. 622

LYTHRACEAE

Ammannia sp.

Galpinia transvaalica N.E.Br.

COMBRETACEAE

Combretum apiculatum Sond.

452, 486

Combretum erythrophyllum (Burch.) Sond.

.. 484

Combretum molle R.Br. ex G. Don

Terminalia phanerophlebia Engl. & Diels.

.. 485

MYRTACEAE

Eugenia capensis Harv.

- * Syzygium guineensis DC.

ONAGRACEAE

Oenothera rosea Ait.

ARALIACEAE

Cussonia sp. possibly C. kraussii Hochst.

.. 594

PRIMULACEAE

Samolus valerandi L.

PLUMBAGINACEAE

Plumbago capensis Thunb.

SAPOTACEAE

<u>Sideroxylon inerme</u> L.	..	472
<u>Mimusops obovata</u> Sond.	..	588
<u>Manilkara concolor</u> (Harv.) Gerstner		

EBENACEAE

<u>Euclea divinorum</u> Hiern		
* <u>Euclea natalensis</u> A. DC.		
<u>Euclea schimperi</u> (A.DC.) Dandy var. <u>daphnoides</u>		
(Hiern) De Winter		
* <u>Euclea shimperi</u> (A.DC.) Dandy var. <u>shimperi</u>		
(Hiern) De Winter		
<u>Euclea undulata</u> Thunb.	..	489
<u>Diospyros dicrophylla</u> (Gand.) De Winter	..	459
<u>Diospyros glandulifera</u> De Winter	..	462
<u>Diospyros lycioides</u> Desf. subsp. <u>sericea</u> (Bernh.)		
De Winter		
<u>Diospyros simii</u> (Kuntze) De Winter		

OLEACEAE

<u>Olea africana</u> Mill.	..	493
<u>Jasminum multipartitum</u> Hochst.	..	590

SALVADORACEAE

<u>Azima tetraacantha</u> Lam.	..	554
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LOGANIACEAE

Strychnos innocua Del. = S. madagascariensis Poir.

Strychnos spinosa Lam.
Nuxia oppositifolia (Hochst.) Benth. .. 497

GENTIANACEAE

Chironia krebsii Griseb.

APOCYNACEAE

Rauvolfia caffra Sond.
Strophanthus gerrardii Stapf .. 501
Wrightia natalensis Stapf .. 650

ASCLEPIADACEAE

Raphionacme elata N.E.Br.
Stomatostemma monteiroae (Oliv.) N.E.Br.
Stomatostemma sp. N.E.Br.
Xysmalobium sp. R.Br.
Ceropegia sp. L.
Emplectanthus cordatus N.E.Br.
Fockea tugelensis N.E.Br.

CONVOLVULACEAE

Ipomoea plebeia R.Br. subsp. africana Meeuse

BORAGINACEAE

Cordia ovalis R.Br.
Ehretia rigida (Thunb.) Druce .. 483
Heliotropium ciliatum Kaplan
Heliotropium nelsonii C.H.Wright
Heliotropium steudneri Vatke .. 531
Heliotropium strigosum Willd.
Trichodesma augustifolium Bak.

VERBENACEAE

Chascanum hederaceum (Sond.) Moldenke
Chascanum schlechteri (Güicke) Moldenke .. 612

LABIATAE

<u>Leucas glabrata</u> R.Br.	
<u>Hyptis pectinata</u> Poir.	
<u>Coleus</u> sp. Lour.	.. 555
<u>Becium</u> sp. Lindl.	
<u>Orthosiphon australis</u> Vatke	.. 532

SOLANACEAE

<u>Lycium acutifolium</u> E. Mey.	
<u>Lycium</u> sp. L.	.. 607
<u>Solanum panduraeforme</u> E.Mey.	
<u>Solanum coccineum</u> Jacq.	

SCROPHULARIACEAE

<u>Selago racemosa</u> Bernh.	
<u>Veronica anagallis-aquatica</u> L.	
<u>Striga gesnerioides</u> Vatke	
<u>Striga thunbergii</u> Bth.	

BIGNONIACEAE

<u>Tecomera capensis</u> (Thunb.) Spack.	.. 455
* <u>Kigelia africana</u> (Lam.) Benth.	

PEDALIACEAE

<u>Ceratotheca triloba</u> (Bernh.) Hook.f.	
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ACANTHACEAE

<u>Thunbergia dregeana</u> Nees	.. 598
<u>Thunbergia atriplicifolia</u> E.Mey.	.. 606
<u>Chaetacanthus burchellii</u> Nees	.. 636
<u>Ruellia patula</u> Jacq.	.. 530
<u>Lepidagathis scabra</u> C.B. Cl.	
<u>Barleria elegans</u> S.Moore	
<u>Barleria obtusa</u> Nees	
<u>Blepharis integrifolia</u> (L.f.) E.Mey.	.. 635
<u>Crossandra fruticulosa</u> Lindau	.. 527a
<u>Crossandra greenstockii</u> S.Moore	

<u>Asystasia</u> sp. Blume	..	634
<u>Dicliptera chinopodia</u> Nees		
<u>Ecbolium amplexicaule</u> S.Moore	..	633
<u>Justicia flava</u> (Vahl) Vahl	..	528
<u>Justicia petiolaris</u> G.Mey.		
<u>Justicia protracta</u> (Nees) T.Anders.		

RUBIACEAE

<u>Kohautia</u> sp. probably <u>Kohautia caespitosa</u> Schuizlein		
<u>Kohautia virgata</u> (Willd.) Brem.		
<u>Xeromphis obovata</u> (Hochst.) Keay		
<u>Xeromphis rudis</u> (E.Mey.ex Harv) Codd		
<u>Gardenia spatulifolia</u> Stapf & Hutch.	613,	625
<u>Canthium setiflorum</u> Hiern	..	516
<u>Canthium spinosa</u> L.	..	621
<u>Plectroniella armata</u> (K.Schum.) Robyns	..	454
<u>Dinocanthium hystrix</u> Brem.	..	476
<u>Pavetta delagoensis</u> Brem.		
<u>Pavetta gracilifolia</u> Brem.		

CUCURBITACEAE

Cucumis metuliferus E.Mey.

CAMPANULACEAE

Lobelia filiformis Lam. var. natalensis (A.DC.)
E. Wimm.

COMPOSITAE

<u>Vernonia capensis</u> (Houtt.) Druce	..	630
<u>Veronia fastigiata</u> Oliv. & Hiern.		
<u>Ageratum conyzoides</u> L.		
<u>Aster luteus</u> Hutch.	..	637
<u>Aster muricatus</u> Less.	..	638
<u>Nidorella resedifolia</u> DC.	556,	602
<u>Brachylaena ilicifolia</u> (Lam.) Phill. & Schweick		
<u>Tarchonanthus camphoratus</u> L.		
<u>Tarchonanthus galpinii</u> Hutch. & Phill.	..	502
<u>Tarchonanthus minor</u> Less.	..	560
<u>Tarchonanthus trilobus</u> DC.		
<u>Blumea caffra</u> (DC.) O.Hoffm.		
<u>Pluchea dioscorides</u> DC.	..	453
<u>Sphaeranthus peduncularis</u> DC.		

<u>Gnaphalium luteo-album</u> L.	
<u>Helichrysum leptolepis</u> DC.	
<u>Helichrysum nudifolium</u> (L.) Less. var. <u>leiopodium</u> (DC.) Moes.	
<u>Helichrysum rugulosum</u> Less.	500, 611
<u>Helichrysum undatum</u> Less.	412
<u>Pulicaria scabra</u> (Thunb.) Druce	
<u>Zinnia peruviana</u> L.	
<u>Flaveria bidentis</u> (L.) Kuntze	.. 570
<u>Schkuhria pinnata</u> (Lam.) Kuntze	.. 559
<u>Cotula anthemoides</u> L.	
<u>Senecio bupleuroides</u> DC.	
<u>Senecio inaequidens</u> DC.	
<u>Senecio</u> sp. aff <u>S. barbertonicus</u> Klatt	
<u>Senecio viminalis</u> Brem.	
<u>Berkheya erysithales</u> (DC.) Roessl.	

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APPENDIX III

A SYSTEMATIC LIST OF THE LARGER MAMMALS IN
UMFOLOZI GAME RESERVE.

COMPILED BY MR. O. BOURQUIN.

Tubulidentata

Antbear

Orycteropus aferPrimates

Chacma baboon

Papio ursinus

Large grey bush baby

Galago crassicaudatus

Vervet monkey

Cercopithecus aethiopsCarnivora

Black backed jackal

Canis mesomelas

Striped polecat

Ictonyx striatus

Honey badger

Mellivora capensis

Civet

Viverra civetta

Rusty spotted genet

Genetta rubiginosa

Slender mongoose

Herpestes sanguineus

Water mongoose

Atilax paludinosus

Dwarf mongoose

Helogale parvula

Banded mongoose

Mungos mungo

Giant mongoose

Ichneumia albicauda

Yellow mongoose

Cynictis penicillata

Aardwolf

Proteles cristatus

Spotted hyaena

Crocuta crocuta

Serval

Felis serval

Leopard

Panthera pardus

Lion

Panthera leo

Cheetah

Acinonyx jubatusPerissodactyla

Black rhinoceros

Diceros bicornis

Squarelipped rhinoceros

Ceratotherium simum

Burchell's zebra

Equus burchelli

ABSTRACT

A landscape unit approach based on use of airphotos was used for investigation of Deciduous Acacia Woodland in the Reserve. The approach was useful for indicating that a quantity of as few as 531 samples could be suitable for sampling woody vegetation over the large, 493 km² area, and for showing where the samples might advantageously be distributed. Use of the approach minimised the extrapolation of community boundaries for mapping purposes.

Normal association analysis of the samples revealed the nine woody consociations present and provided quantitative data on species constancy and fidelity. These data were used towards explaining low levels of homogeneity within consociations, as well as some close floristic similarities found between consociations. The successful emergence of a species to dominance in a consociation was ascribed to the presence of a particular, described soil series or rock substrate. The distribution pattern of the consociations resembled a soil-vegetation catena on the landscape. The consociations were grouped into defined physiognomic categories of Open, Closed and Riverine Woodland Associations that were distributed according to three soil associations. The effects of soil factors, fire and the biota on physiognomy, notably secondary thicket encroachment, were discussed; and the relationship between climate and phenology was mentioned.

A quantitative description of the grass communities based on normal analysis of stratified sample data revealed a retrogression whereby climax grasses are being replaced by mid-seral and pioneer grasses. The retrogression was ascribed to selective grazing by an increasingly large biomass of enumerated, indigenous herbivores. Some of the management recommendations offered were based on empirically calculated estimates of the weights of dry grass required annually by the grazing animals.

Copies of topography, place names, geology, land

surface and vegetation maps are provided. The text is supplemented by check lists of plants and animals recorded, by eight figures, 33 tables and 54 photos.

* * * * *

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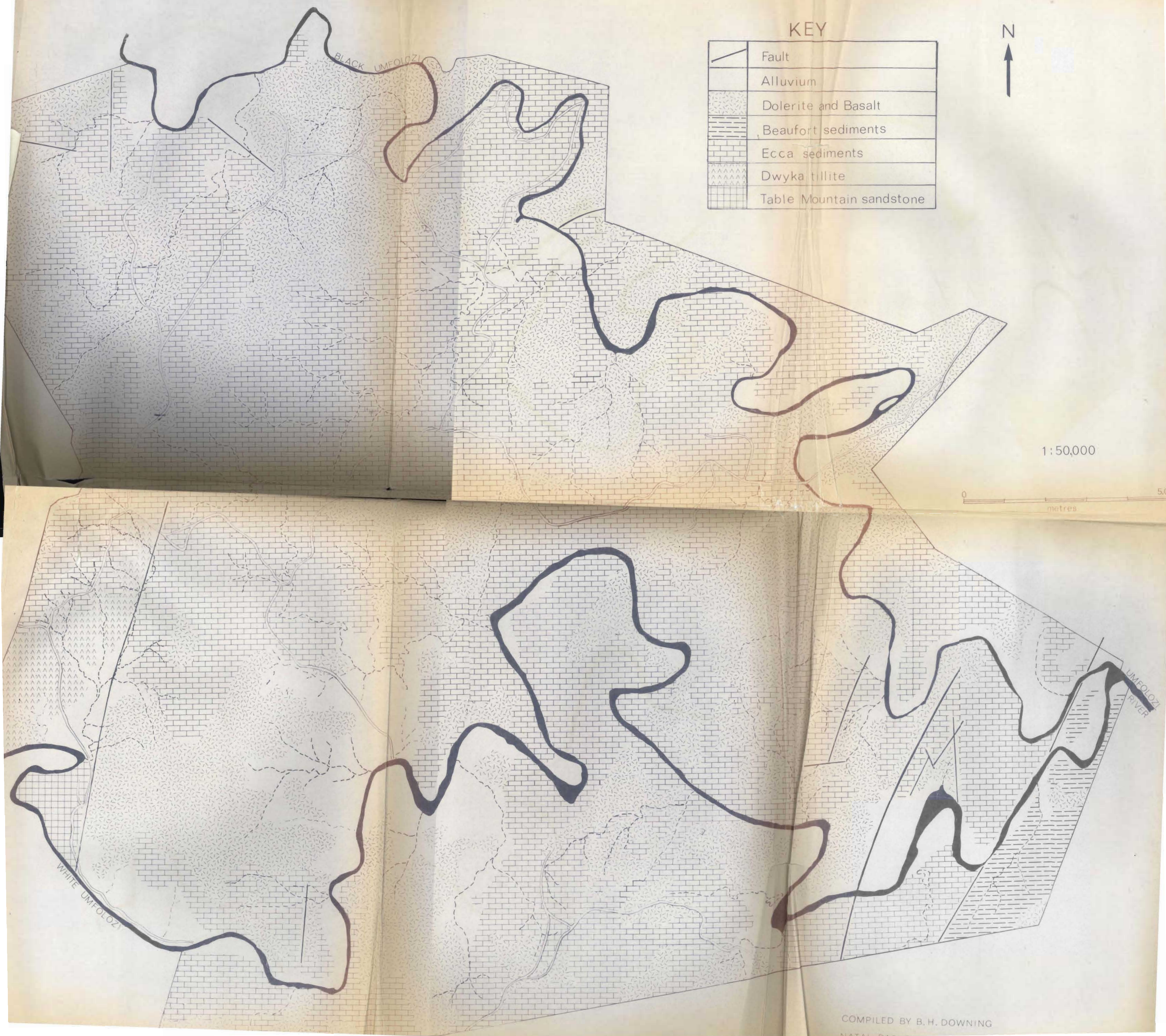
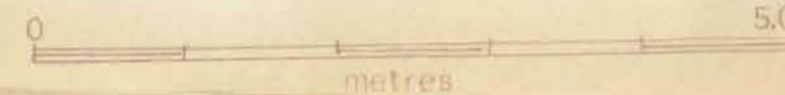
UMFOLOZI GAME RESERVE

KEY

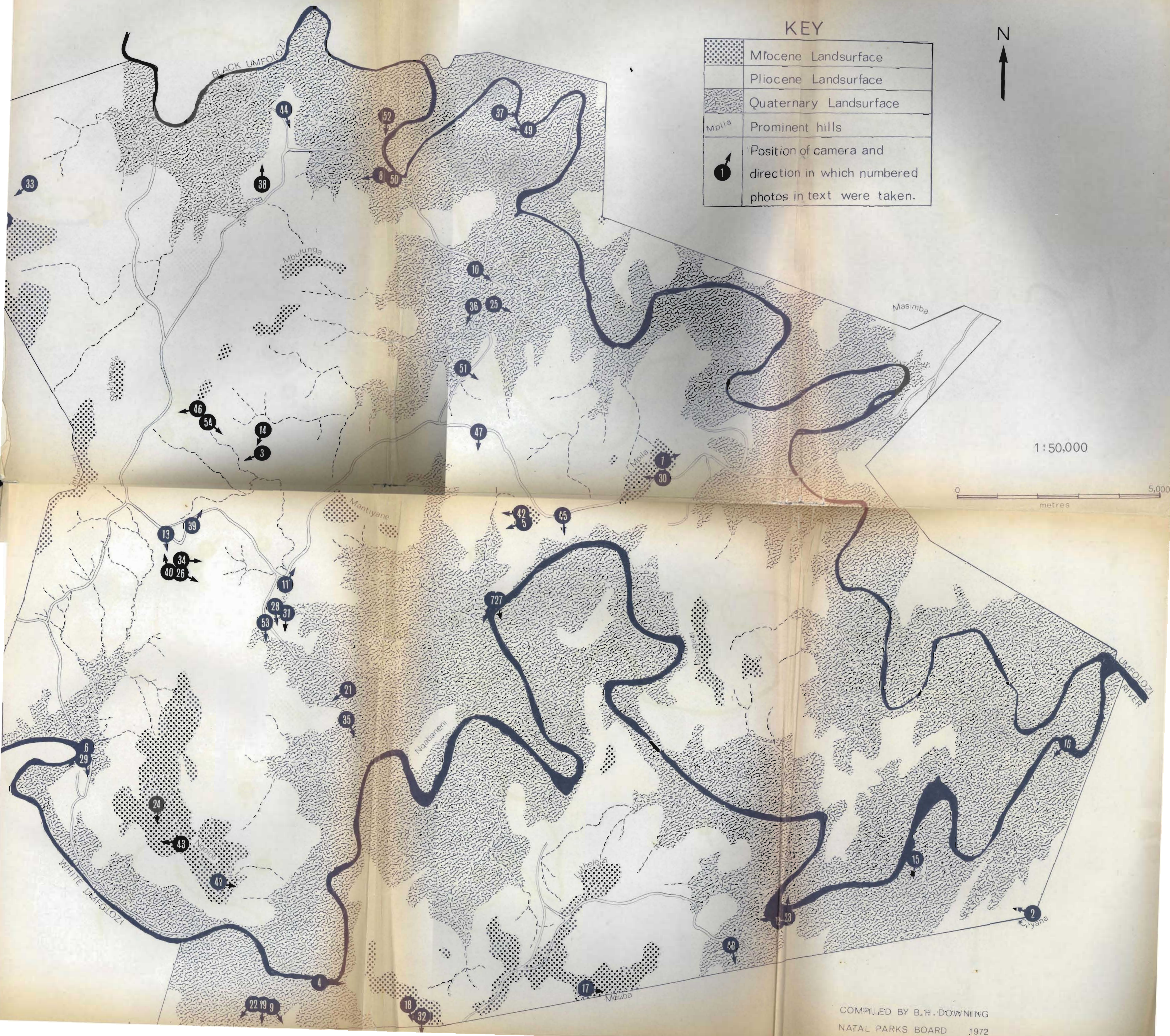
	Fault
	Alluvium
	Dolerite and Basalt
	Beaufort sediments
	Ecca sediments
	Dwyka tillite
	Table Mountain sandstone



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UMFOLOZI GAME RESERVE



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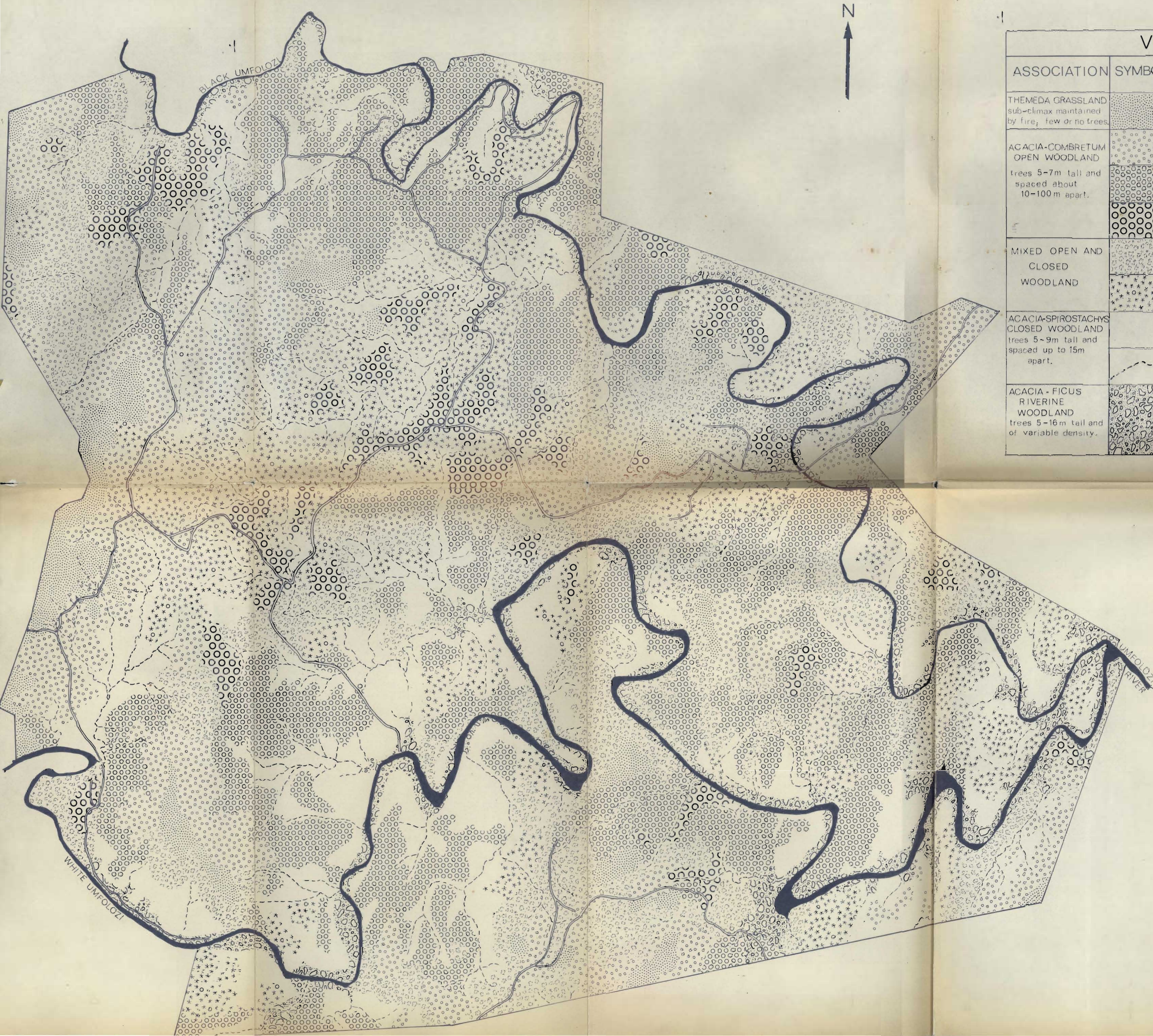
	Mfocene Landsurface
	Pliocene Landsurface
	Quaternary Landsurface
	Prominent hills
	Position of camera and direction in which numbered photos in text were taken.

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VEGETATION MAP OF DECIDUOUS ACACIA WOODLAND
UMFOLOZI GAME RESERVE



KEY

VEGETATION				SOILS	
ASSOCIATION	SYMBOL	WOODY COMMUNITY	PRINCIPAL GRASSES	TYPE	ASSOCIATION
THEMEDA GRASSLAND sub-climax maintained by fire, few or no trees.	[stippled]	occasional, small stands of <i>Acacia caffra</i>	<i>Themeda triandra</i> <i>Cymbopogon</i> spp. <i>Digitaria macroglossa</i>	Stony soils, often steep terrain.	Shallow, leached UPLAND SOILS
ACACIA-COMBRETUM OPEN WOODLAND trees 5-7m tall and spaced about 10-100 m apart.	[circles]	<i>Acacia tortilis</i>	<i>Panicum deustum</i> <i>Panicum coloratum</i>	Dark, red-brown clays of KIAORA form.	
		<i>Acacia nigrescens</i>	<i>Themeda triandra</i> <i>Panicum coloratum</i>	Pale grey sands of SPRINGFIELD series.	
MIXED OPEN AND CLOSED WOODLAND	[stars]	<i>Combretum apiculatum</i>	<i>Themeda triandra</i> <i>Aristida barbicolis</i>	Mixed bouldery soils of MISPAH series.	Deep, lime rich, easily eroded BOTTOMLAND SOILS
		<i>Acacia nilotica</i>	<i>Urochloa mosambicensis</i> <i>Panicum</i> spp. <i>Sporobolus</i> spp.	Dark black clay of ARCADIA series Dark grey clay of UITVLUGT series.	
ACACIA-SPIROSTACHYS CLOSED WOODLAND trees 5-9m tall and spaced up to 15m apart.	[dots]	<i>Acacia grandicornuta</i>	<i>Tragus berteronianus</i> <i>Dactyloctenium australe</i>	Orange and red clays of HUTTON form.	
ACACIA-FICUS RIVERINE WOODLAND trees 5-16m tall and of variable density.	[wavy lines]	<i>Spirostachys africana</i>	<i>Phragmites</i> spp. <i>Panicum meyerianum</i> <i>Panicum maximum</i> <i>Cynodon dactylon</i>	Dark clay soils e.g. BONHEIM & RENSBURG series.	Deep, perennially moist and sandy RIVERINE SOILS
		<i>Acacia robusta</i> <i>Phoenix reclinata</i>		Pale alluvia	

1:50,000

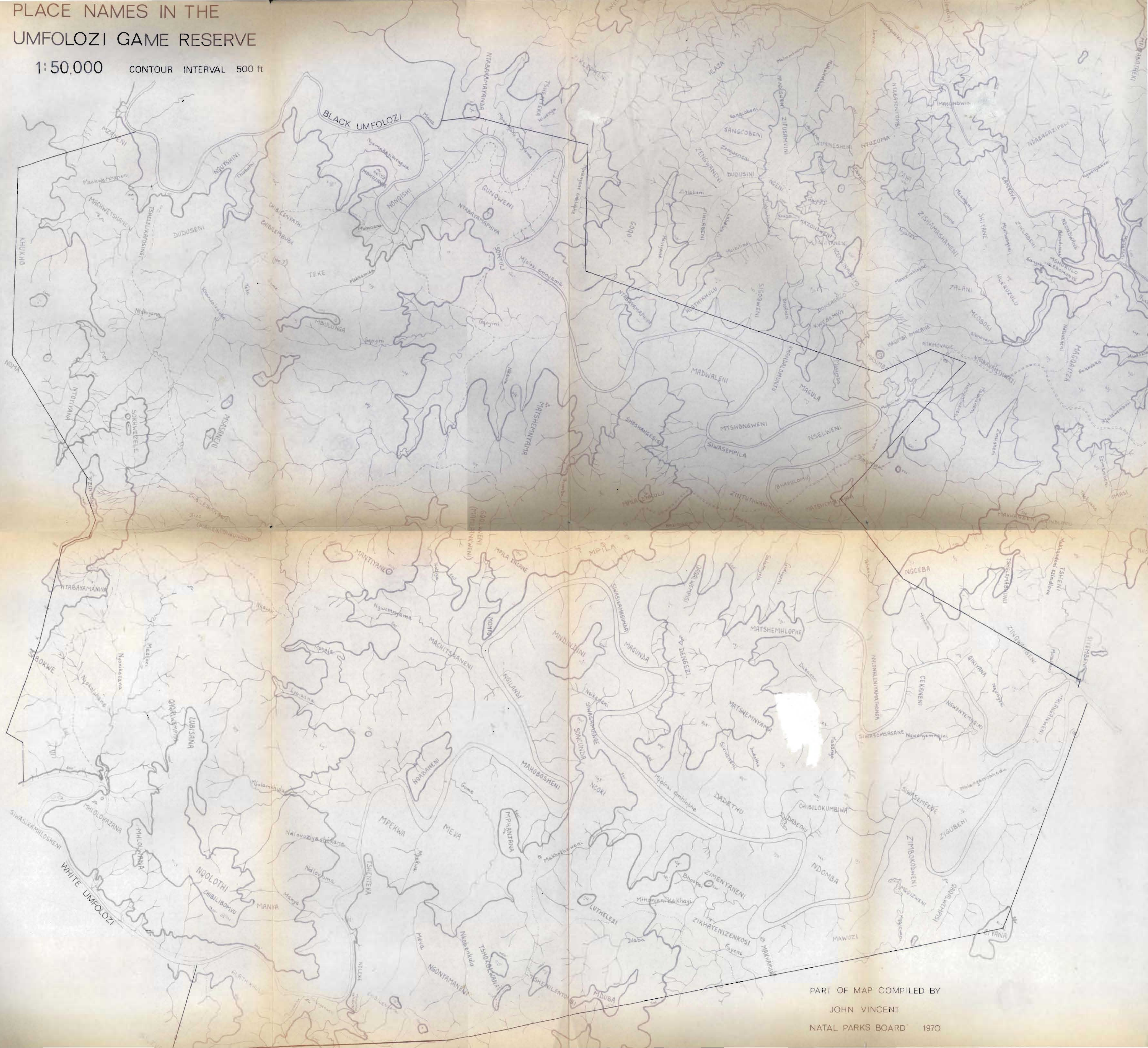


COMPILED BY B.H. DOWNING
NATAL PARKS BOARD 1972

PLACE NAMES IN THE UMFOLOZI GAME RESERVE

1:50,000

CONTOUR INTERVAL 500 ft



PART OF MAP COMPILED BY

JOHN VINCENT

NATAL PARKS BOARD 1970

