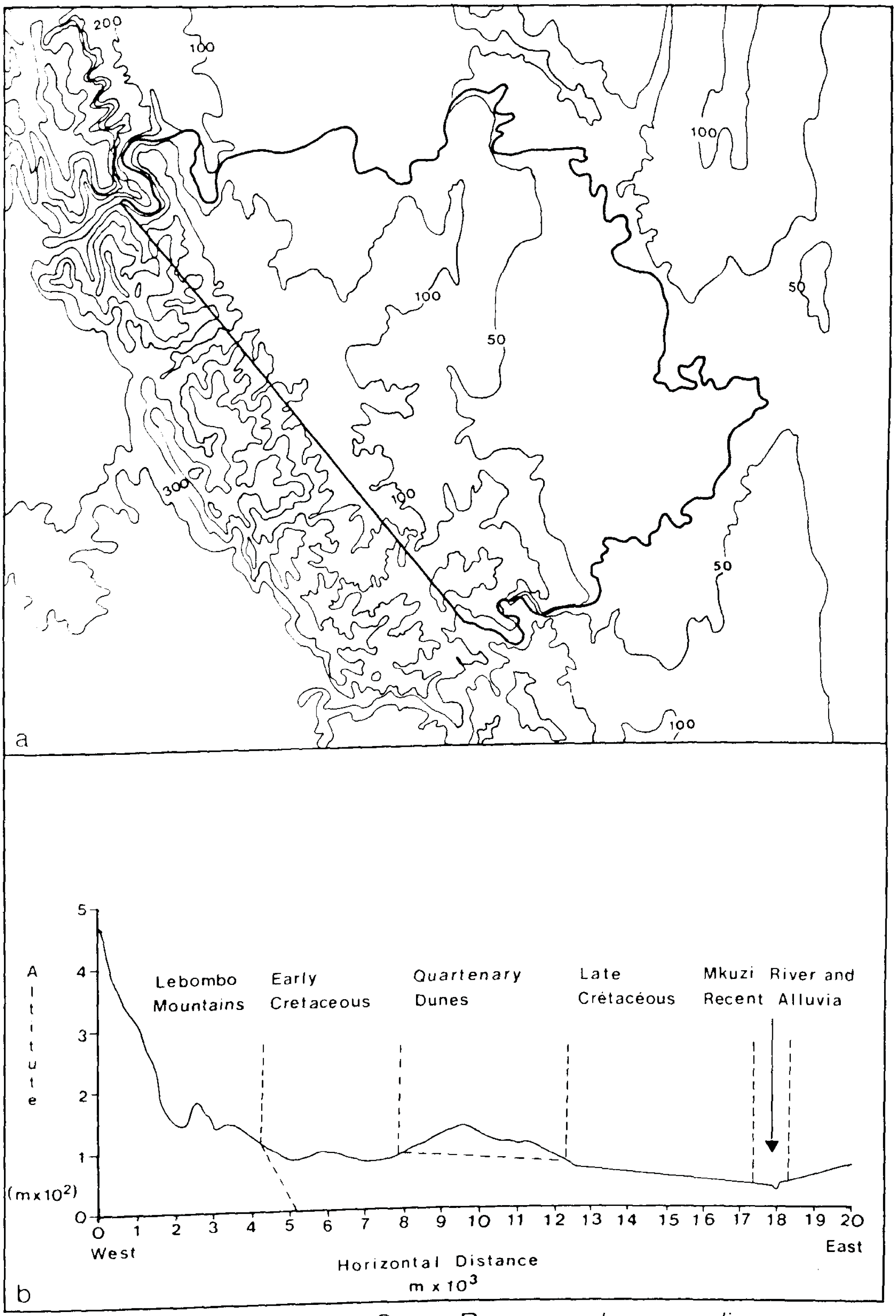


Fig. 4a Topograpy of Mkuzi Game Reseve and surrounding areas.

Fig. 4b A cross-section through the game reserve illustrating the gross strategraphic relationships and major topographic features.

are acid extrusive rocks which due to their extreme resistance to erosion, have given rise to the Lebombo Mountains (King, 1963). The latter rise approximately 450 m above the surrounding basaltic and Cretaceous plains, which occur to the west and east respectively.

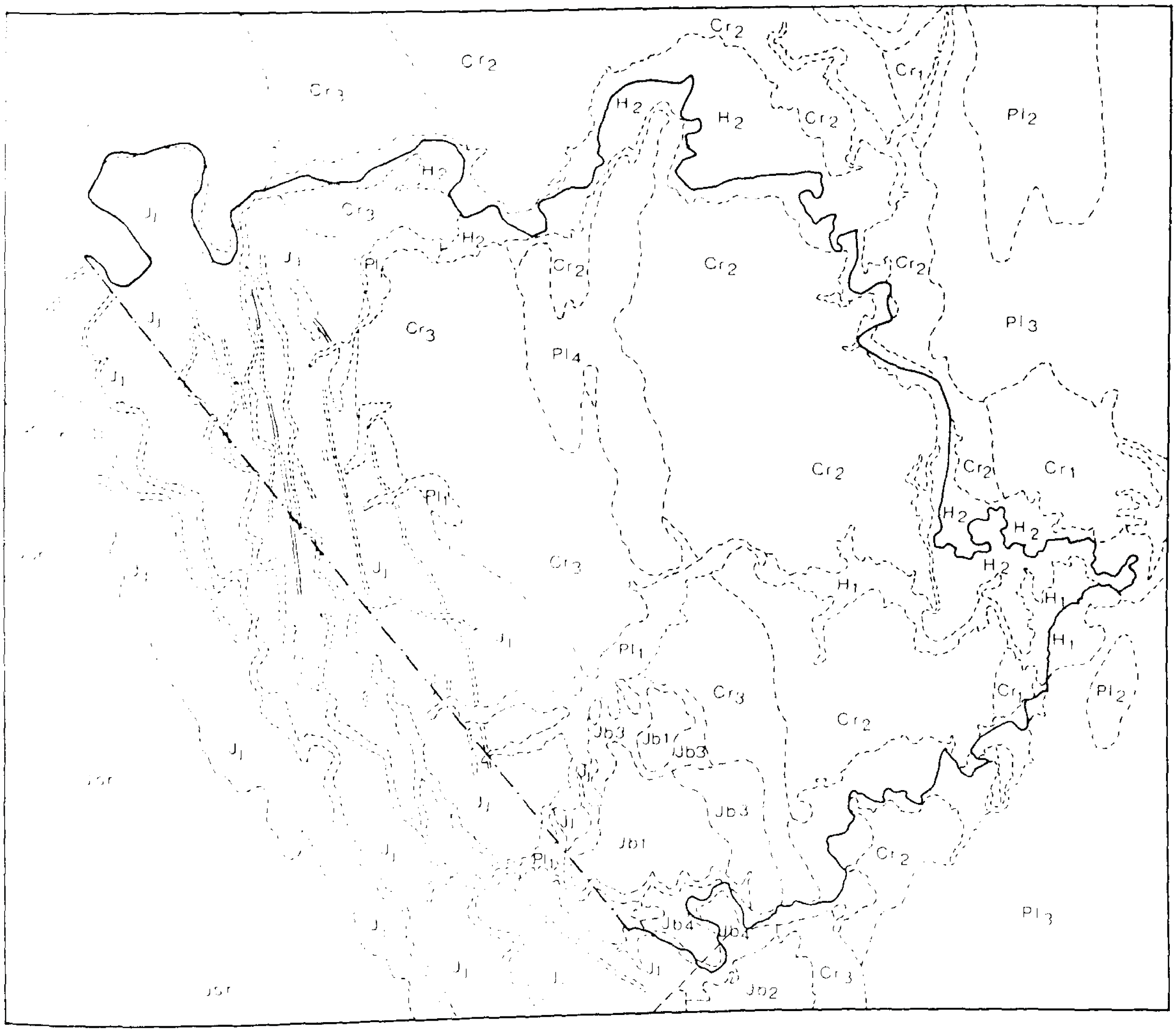
Two further volcanic bodies occur in a restriced area in the south of the reserve (overlying and slightly east of the Jozini formation). They are the Mpilo Member Basalts and the Bumbeni Complex (Fig. 5). The former, underlie the latter and consist of a succession of poorly exposed basaltic to andesitic amygdaloidal lavas. The Bumbeni Complex is larger and more varied and consists mainly of intrusive and extrusive rhyolite lava (Bristow, 1976). East of the main exposures of rhyolitic flow is an area of perlitic pitchstone, air-fall tuffs and volcanic breccia. Their extreme easterly location, and the fact that Cretaceous rocks are found a few hundred metres further east, indicates that they formed part of the final minor eruptions signifying the closure of the Lebombo volcanic event which had lasted almost 50 million years (m.y.) (Bristow, 1976).

The Lebombo volcanics and their closure were intimately related to the break-up of the protocontinent Gondwanaland. Along the east coast of Africa, marine incursions extended gradually southward along the continental rift and are recorded as Early Cretaceous deposits in Mocambique and Zululand (Hobday, 1979). At this time, and as may be evidenced today, the Lebombo volcanics were steeply tilted as a series of blocks in an eastward direction (Maud, 1980).

The early and late cretaceous conglomerates and sediments which underlie the rest of the reserve and the Zululand coastal plain were deposited on the down warped margins produced by the breakup of Gondwanaland (Fig. 5). These deposits probably originated in the beds of high gradient, anastomosing, torrential streams. Most of the rocks of the eroded hinterland, including basalt, dolerite, rhyolite, granite banded ironstone and quartzite are represented. There is an upward and seaward (west to east) gradation of sedimentary material which ranges from a predomimance of boulders, to pebbles, cross-bedded sands, marls and silts (Hobday, 1979). The lower (early) Cretaceous Period lasted from about 140 m.y. to 100 m.y. ago).

Following the break up of Gondwanaland and the separation of the southern continents, the southern African subcontinent underwent a series of uplifts associated with concomitant down flexing of the margins (King and King, 1959). Depending upon the position of the axis of no relative movement, these tectonic events were responsible for either emergence of the coastal margins (axis seaward of the coastline) or marine transgression (axis inland). King and King (1959) have postulated marginal tilting during the mid- Cretaceous, early Miocene, early Pliocene, and end Pliocene - early Pleistocene. In addition to these tectonic changes in the relative levels of land and sea, there were world-wide, sea-level changes due to glacio-eustatism. Thus, from the end of the Cretaceous through the Tertiary and Quartenary periods, the coastal plain underwent a complex history of sedementation and erosion, related to marine transgressions and regressions. During each regression, stratified marine deposits from the last transgressive phase were re-worked, eroded and redistributed by marine and subaerial agencies in the form of loose sand cover and dunes. This sequence of events has resulted in the prominent north - south trending dune ridges which are conspicuous topographic features of the present day coastal plain.

These dunes are generally composed of red or yellow-brown sand with a boulder bed commonly present at the base of the western cordon giving way eastward to scattered pebble horizons. Davies (1976) has mapped this series of dune cordons which he has aged from archaeological evidence. His work indicates a decrease in age from west to east and he assumes that each cordon was constructed in the vicinity of the contemporary shore. The oldest shore line resulting in the innermost (most westerly) dune cordon is speculated to be of Plio-Pleistocene age, and occurs adjacent to the Lebombo volcanics in the game reserve (Fig. 5). This ridge is poorly preserved, with generally well developed soil profiles which are commonly deep red, displaying advanced mineral diagenesis. The red colour is epigenic and is due to a coating of iron oxides around the sand grains, which were probably derived from the breakdown of ferro-magnesium minerals. In general these sands contain feldspar which has become partly kaolinized. This mineral breakdown becomes less pronounced seaward (Hobday, 1979).



Geological Period		Lithology and Formation	Symbol
Quaternary	Holocene	Marsh	H_1
		Young alluvium	H_2
	Pleistocene	Old alluvium	Pl_1
		Red dune cordon sand	Pl_2
	Pliocene	Argillaceous sand	Pl_3
		Orange to red dune cordon sand	Pl_4
	Cretaceous	Siltstone and sandstone	Cr_1
		Glauconitic marine sandstone with shelly concretions	Cr_2
		Conglomerate, grits, sandstone, siltstone.	Cr_3
Jurassic	Bumbeni Complex	Rhyolite and pyroclastic rocks	Jb_1
		Syenite, micro-syenite, granite, granodorite	Jb_2
		Rhyodacite and brecci, rhyolite and porphyry agglomerate, tuff with bombs, volcanic glass, tuff breccia and perlite.	Jb_3
		Amygdaloidal basalt (Mpilo member).	Jb_4
		Conglomerate and sandstone (Msundusi)	Jm
		Rhyodacite with pyroclastic flows — J_{11}	J_1
		Vesicular acid lava, — J_{12}	J_1
		Basalt and andesite — J_{13}	J_1
		Basalt (Sabi River)	Jsr

Fig. 5 Geological map of Mkuzi Game Reserve and surrounding areas.

The next dune cordon, which is approximately 2 km seaward (east), is slightly lower and better preserved than the first. Davies (1976) has assigned this cordon to the antipenultimate interglacial high water level and subsequent glacial regression. This cordon forms a prominent ridge bisecting the reserve (Fig. 5), and soil profiles are generally poorly developed compared to those of the first dune.

The next dune cordon, attributed to the penultimate glaciation, occurs 11 km to the east of the last and is situated outside the reserve. The Mkuze and Msunduzi Rivers incise this dune cordon to the east of the reserve and thus during the upper Pleistocene the area to the west of this cordon (i.e. the eastern low lying portion of the reserve) would have been estuarine. Marine and river-borne sediments would have been deposited here.

The last glaciation, with three interglacial peaks of sea level, was followed by a deep regression. This regression attained several distinct minima of over 100 m below the present level. Rejuvenation of the lower courses of coastal rivers resulting from the lowered base level, caused deep valley incision and it is postulated that practically all of the older valley fill relating to the previous glaciation was eroded (Hobday, 1979). Following the Pleistocene eustatic low (17,000 years before present (B.P.)), climatic amelioration was accompanied by rapid transgression until about 10 000 years B.P. (the Pleistocene-Holocene boundary), when there was a decrease in the rate of sea-level rise. During this period of upper-Pleistocene and lower-Holocene transgression, the effect of the gradually rising base level was to cause infilling of previously incised coastal river valleys. The closing event in the geological history of Mkuzi was thus the deposition of alluvial material along the incised drainage lines and the creation of pans, reed swamps and vleis where these drainage lines became submerged (Fig. 5).

2.4 SOIL

Prior to the commencement of this study, no detailed work had been undertaken on the soils of Mkuzi. The description made here corresponds more or less to a group level of abstraction. The detailed analysis is presented later. In general soils correspond closely to underlying geology and topography, but the complicated minerological composition of the interface between the Stormberg lavas and the early cretaceous conglomerates makes precise interpretation difficult in this area.

To the west of the reserve, the combination of relatively steep slopes and the erosion resistant fine grained, felsic crystalline rocks of the Lebombo Mountains, have given rize to lithosols of various depths. The incised valley floors are generally angular with the area of alluvial deposition small. These alluvia are predominantly shallow gritty clays with the clay complex dominated by kaolinite.

Early cretaceous geological deposits consisting of conglomerates, grit, sandstones and siltstones (derived from a variety of rock types including basalt, dolerite, rhyolite, granite, banded ironstone and quartzite) have resulted in soils of varying depths, texture and minerological composition. Weathering and erosion have resulted in a landform that is gently undulating (slope angles 2 - 5 ^{o}), with moderate relief (valley depth 30 - 100 m) and moderate drainage spacing (400 - 1500 m). Both interfluves and valley floors are rounded resulting in convex-concave slopes. In general, soil depth and clay content increases from west to east and from upland to valley floor. Upland sites are characterised by lithic soils in the west and ferruginous soils in the east, while bottomlands are generally calcimorphic, characterised by brown to dark brown calcimorphic soils in the west and vertisols in the east. Upland soils are more leached and have a clay fraction consisting predominantly of 1:1 lattice minerals whilst their bottomlands are relatively unleached with high base saturation and an appreciable proportion non-expanding 2:1 lattice clay minerals.

Late Cretaceous geological deposits occurring to the east of the reserve (Figs. 4 and 5), consist primarily of glauconitic sandstone (quartzitic sandstone rich in hydrous potassium silicate) and have resulted in a uniformly deep soil mantle throughout the area. The landform is level to very gently sloping (0 - 2 °) with a very low (<10 m) relative relief, wide (1 500 - 3 000 m) drainage spacing orientated from north to south and a profile form which features flat, interfluves in conjunction with angular valley floors. Calcimorphic clay to sandy clay loam soils predominate throughout this region, the flat interfluves being characterized by brown calcimorphic sandy clay loams in which the clay fraction is dominated by 1:1 and non-expanding 2:1 lattice clay minerals. Valley floors have a higher proportion of clay, which increases from north to south, as does the proportion of expanding 2:1 lattice clay minerals. Vertisols are common on this land unit and dominate in the extreme south adjacent to Nsumu Pan, where they occur in the form of a wavy gilgai. Scattered throughout this region and restricted to shallow, pan forming depressions, are weakly formed, hydromophic gley soils. Although these soils are not important in extent, their existance and distribution do affect distribution of wet season water sources.

Quarternary sand deposits occur as two parallel dune cordons which bisect the reserve and are orientated roughly north-south (Figs. 4 and 5). On the older, most westerly occurring dune, soil profiles are generally deep, red and well developed displaying advanced mineral diagenesis. Soils in upland sites are classified as ferruginous arenosols. Due to their higher proportion of kaolinitic clay, those soils lower down the catenary sequence are classed as ferruginous soils. On the younger, eastern, dune, soil profiles are generally a poorly developed yellow to orange arenosol. At places al ong the margin of this dune cordon, slightly above the area where the cretaceous deposits emerge from beneath the quarternary sand mantle, a seep zone occurs below which is a region of predominantly duplex calcimorphic soils.

Geological alluvia (those fluvial, lacustrine or marine strata deposited since the Holocene) in Mkuzi have given rise to a number of soil types depending on the nature of the deposit and the time since deposition. There are a large number of soils derived from alluvium which are no longer subject to flooding, and in which appreciable horizon development has taken place. Thus, in some of the "older alluvia", a structural B-horizon is not uncommon and classifying these as ferruginous, eutrophic soils would not be out of place. However, the term alluvial soil is used here in the broader sense, genetically defined as soils derived from alluvium, including calcimorphic and gleyed profiles, but excluding alluvially derived vertisols and halomorphic soils (Young, 1976).

Large expanses of alluvial soil occur adjacent to the two major rivers, the (Mkuze and Msunduze) and major streams the Nhlohlela and Nsumu (Fig. 5). Other alluvial soils occur as fans of minor drainage channels originating in the Lebombo Mountains and small plains adjacent to minor streams. With the exception of the lower sections of the Mkuze and Msunduze rivers, all these alluvia are no longer subject to flooding and various amounts of horizon development has taken and is still taking place.

2.5 SURFACE HYDROLOGY

The combination of climatic (low rainfall, high evaporative demand) and geomorphological factors has resulted in an area with no naturally occurring permanent surface water resources within its boundaries. The two major rivers which form the northern and eastern (Mkuze) and southern (Msunduze) boundaries of the reserve arise and have the major portions of their catchments to the west of the reserve. At present the water flow in these rivers is seasonal and dependent to a large extent on rainfall in the catchment and consumptive use before the rivers reach the reserve. There is little evidence as to whether either of these rivers was permanent in the recent past, but due to the sandy nature of their beds it would seem unlikely. Subsurface water however, is available from the bed of the Mkuzi river throughout the year. The reserve itself and the eastern Lebombo Mountains between the Mkuze and Msunduzi rivers are drained by numerous easterly flowing seasonal streams, the majority of which anastomose forming two major streams the Nhlohlela and the Nsumu, which drain via the Nhlohlela (c. 47 ha) and Nsumu (c. 250 ha) pans into the Mkuze River (Fig. 1).

Numerous small (less than 0,25 ha), shallow clay floored seasonal pans occur throughout the reserve but are particularly common in the eastern half. Several larger (up to 250 ha) pans occur along the Mkuze river floodplain. Most of these may be filled via channels from the Mkuzi River and/or via streams which drain the reserve. The largest of these is in the Nsumu Pan in the south eastern corner of the reserve close to the confluence of the Mkuze and Msunduzi rivers. Artificial watering points consist of ten dams and, in two instances, water piped to two pans, Bube and Msinga, in the center of the reserve (Fig. 1). Water in Bube and Msinga pans constitutes the only permanent supply to animals as all the dams are to a greater or lesser extent seasonal.

2.6 VEGETATION AND FAUNA

Mkuzi falls into two major phytochorological regions, namely the Indian Ocean Coastal Belt and more particularly a subdivision of this, the Tongaland - Pondoland Regional Mosaic (Werger, 1978; Moll and White, 1978) and the Sudano-Zambezian Region (Werger, 1978; Werger and Coetzee, 1978). The area is considered by White (1976) to be both a Regional Transition Zone and a Regional Mosaic, having a high proportion of endemics. According to Acocks (1975), Mkuzi is representative of three veld types: 1 - Coastal Forest and Thornveld, 10 - Lowveld (one of the Tropical Bush and Savanna Types) and 6 - Zululand Thornveld.

Other than some notes by Moll (1968) no description of the vegetation of Mkuzi exists. Descriptions at the regional level are made in Werger and Coetzee (1978), Moll and White (1978) and Moll (1980).

Mkuzi may be divided into nine major vegetation types which overlap along complex environmental gradients and thus are not in all instances distinct. They are:-

1. Dry Mountain Bushveld (Werger and Coetzee, 1978) and Grassland. This is an open woodland to grassland type dominated by *Combretum apiculatum*, *Acacia nigrescens*, *Themeda triandra*, *Heteropogon contortus* and *Cymbopogon excavatus*, and is associated with the lithosols on the Lebombo Mountains.

2. Microphyllous Thorny Plains Bushveld (Werger and Coetzee, 1978), which is represented by *Acacia nigrescens* Tropical Plains Thornveld. It is associated with vertic and ferruginous clay soils in the west and vertic clays in the east of the reserve. The tree layer is dominated by *Acacia nigrescens* with *Dichrostachys cinerea* commonly

in the sub-story. The herbaceous layer is diverse with *Themeda triandra, Panicum coloratum, Panicum maximum, Digitaria eriantha, Urochloa mosambicensis* and *Bothriochloa insculpta* as dominant grasses.

3. Mixed Bushveld (Moll, 1980), consists of a mosaic of woodland types on soils ranging from brown, calcimorphic sandy clay loams to vertic clays and hydromorphic gley soils. The physiognomy is an open to closed woodland, dominated to various degrees by *Acacia tortilis, Acacia nilotica, Acacia grandicornuta* and *Acacia senegal*. Associated trees and shrubs are *Spirostachys africana* and *Schotia brachypetala*. The herbaceous layer is not well developed, the main grasses being *Dactyloctenium australe, Chloris virgata, Eragrostis rigidior* and *Aristida spp.*.

4. Thicket (Moll, 1980). Thickets generally occur on vertic clays and hydromorphic gley soils where topography is flat and soils poorly drained. This vegetation type is generally 3 - 4 m high and, in some places, impenetrable. The two dominant woody species are *Acacia luederitzii* and *Euclea divinorum*. Important grasses include *Dactyloctenium australe, Enteropogon monostachyos, Panicum maximum* and *Panicum deustum*. In places trees such as *Spirostachys africana, Schotia brachypetala, Pappea capensis, Sideroxylon inerme, Berchemia zeyheri, Albizia anthelmintica* and *Cassine spp.* emerge above the thicket forming a dense, multilayered woodland.

5. Red Sand Bushveld (Moll, 1980). Occurring on the ferruginous arenosols of Quarternary origin, this type is essentially an open to closed woodland approximately 7 m tall. The most common tree species are *Combretum molle, Acacia burkei, Sclerocarya caffra, Ziziphus mucronata* and *Terminalia sericea*. The herbaceous layer is generally fairly sparse the most common species being *Dactyloctenium australe, Aristida spp., Panicum maximum, Eragrostis rigidior, Eragrostis pallens, Pogonarthria squarrosa* and *Hyperthelia dissoluta*.

6. Sand forest (Moll and White, 1978; Moll, 1980). A distinctive type of dry, semi-deciduous to deciduous forest occurring on the poorly developed yellow-orange arenosols of Quarternary origin. Sand Forest consists of a mosaic of forest patches 10 to 25 m high in a matrix of open woodland. The most important tree species are *Newtonia hilderbrandtii* (usually in localized pure sands), *Cleistanthus schlechteri, Hymenocardia ulmoides, Pteleopsis myrtifolia, Dialium*

schlechteri, Croton gratissimus and *Strychnos henningsii*. A well-developed sub-canopy of small trees and shrubs consisting mainly of *Salacia leptoclada, Croton pseudopulchellus* and *Hymenocardia ulmoides* is present. The herbaceous ground layer is extremely poorly developed.

7. Riparian fringing forest and woodlands. This may be divided into two principle types:

a) Streambed and drainage line woodland, occurring alongside minor streams and drainage lines. The major woody species are *Schotia bracypetala, Acacia robusta, Spirostachys africana, Euclea schimperi, Sideroxylon inerme, Thespesia acutiloba* and *Cassine spp.*.

b) Riverine forest and woodland, varies from a fairly well-developed forest to an open woodland up to 15 m high and occurs on alluvia adjacent to the two major rivers. The main canopy tree species include *Acacia xanthophloea, Rauvolfia caffra* and *Trichilia emetica*. In places the alien tree *Melia azedarach* forms monospecific stands to the exclusion of indigenous trees. A well developed subcanopy of *Acacia schweinfurthii, Azima tetracantha* and the alien *Eupatorium odoratum* is present in most instances and in places forms impenetrable thickets. The herbaceous layer is usually sparse consisting of a wide variety of forms and creeping grasses.

8. Floodplain grasslands, occur on the seasonally inundated flats adjacent to the Mkuzi and Msunduzi floodplain. The species which characterise this tall grassland are *Phragmites australis, Echinochloa pyramidalis, Eriochloa spp., Sorgum spp.* and *Cyperus spp.*

Zoogeographically, Mkuzi falls into the East African Province of the Ethiopian Region. In many respects the fauna have tropical affinities, and Poynton (1980) comments that for amphibians at least, the region is a zoogeographical transition area between the tropical fauna to the north and non-tropical forms to the south. A list of reptiles found in Mkuzi is reported by Pooley (1965), and again species found in this area have affinities with the Tropical East Coast Littoral, Eastern Tropical Transitional, Western Tropical

Transitional, Tropical Wide Ranging, Temperate Transitional and Cape Temperate Faunal zones (Bruton and Haacke, 1980).

In a recent survey spanning the ten year period between 1970 and 1980, 400 species of birds were recorded in the reserve. Again the area is seen to lie in a transition zone between the Eastern Lowveld, Eastern Tropical Littoral, Eastern Littoral and the Eastern Grass-veld regions (McLachlan and Liversidge, 1978).

The status of mammals for the region (Maputaland) was recently reviewed by Rautenbach, Skinner and Nel (1980) and for the reserve by Dixon (1964). Of major concern to this study are the large mammals and in particular the large herbivores, which are listed approximately in order of decreasing numerical importance. Impala, nyala, warthog, blue wildebeest, kudu, zebra, grey duiker, bushpig, giraffe (introduced), common reedbuck, mountain reedbuck, red duiker, steenbok, suni, black rhinoceros, bushbuck, square-lipped rhinoceros (re-introduced), hippopotomus, eland (re-introduced), waterbuck and klipspringer. Important large herbivores that no longer occur in Mkuzi include elephant and buffalo.

Of the larger predators that occurred in the system, both lion and wild dog, are absent, cheetah have been re-introduced, leopard, spotted hyaena and black-backed jackal are fairly common.

The insect fauna of the reserve and for the region in general is poorly known as is their role in the dynamics of the system.

2.7 PALAEOECOLOGY PAST HISTORY AND LAND USE

The palaeoecology and archaeology of Maputaland (which includes Mkuzi) has been reviewed by Avery (1980) and is summarised very briefly here. First evidence of mans' presence in the game reserve is from the Early Stone Age (Fig. 6) and in this area is likely to be as old as 500 000 BP. This was followed by an industrial complex known as the Middle Stone Age from about 150 000 BP (Fig. 6). The Late Stone Age (40 000 - 50 000 BP) was characterised by more advanced technology and considerable diversification. The bow and arrow was used enabling man to utilize an increasing range of resources. By about 2 000 BP, pottery and in some cases domestic animals were

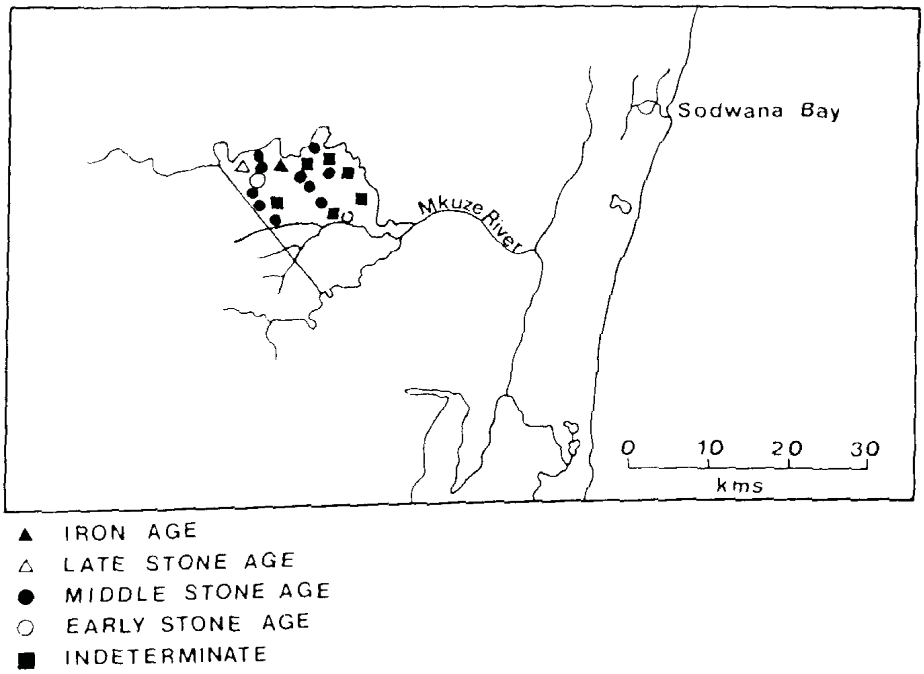


Fig. 6 Distribution of archaelogical sites recorded for Mkuzi Game Reserve and surrounding areas (from Avery, 1980).

introduced and a herding economy, in addition to a hunting-and-gathering subsistence appeared.

By AD 300 negroid herders and cultivators had introduced the Iron Age and it is speculated that modern bantu, with a knowledge of iron-working, pot making, animal husbandry and crop-growing had reached the reserve by about AD 1440 (Bruton, Smith and Taylor, 1980).

Since approximately 200 000 BP the climate had undergone a number of changes. Initially there were at least four changes from warm and wet to temperate, cold and dry or cold and wet. For a period between 95 000 and 75 000 BP the climate was warm and dry, followed by two cold periods separated by a warmer one which was then followed by the present climate (Avery 1980). Throughout his sequence of climatic events, vegetation fluctuated between subtropical forest and tropical savanna.

The large mammal fauna present since the early M.S.A. is listed by Avery (1980) and throughout this period representatives of the present day fauna are shown to have existed then. It is therefore evident that since at least the late Pleistocene (c. 130 000 BP), Mkuzi has evolved in the presence of a full complement of large mammals, including man.

The impact of mans activities on the system as a whole is to a large extent unknown. It is, however, thought that Iron Age people had a significant effect on woodlands and forest through the use of fire to clear lands, improve grazing for domestic stock and through felling of woody plants for domestic uses including iron smelting.

Much of the early history of human involvement in Maputaland since 1500 AD is summarized by Bruton, Smith and Taylor (1980). Apart from the characteristic agricultural practices undertaken by the Bantu occupying Maputaland. The exploitation of the vast herds of game by hunters during the 19th century was of great significance to the biological stability of the area. Baldwin, Drummond, Selous, Dunn, Shadwell and Leslie were some of the well known hunters in the area during that time. Details of abundant herds of eland, kudu, buffalo, nyala, zebra, wildebeest, waterbuck, hippopotamus and impala were left by Drummond (1875) and elephants, rhinoceros and lion were considered common. By 1870 the hunting era was over due to indiscriminate shooting, habitat deterioration and increasing human population pressure. Subsequently, the remaining game populations were drastically reduced by concession hunters and farmers. Between 1900 and 1912, the magistrate stationed at Ubombo (which is to the north of the reserve) took a personal interest in game preservation and the reserve was proclaimed in 1912.

Due to the continuous outbreaks of Trypanosomiasis in domestic stock, health authorities undertook a game eradication programme in the area and in 1917 a total of 25 000 wildebeest were shot in an effort to eradicate the disease. This was however to no avail and in October 1939 control of the reserve was handed over to the Director of Veterinary Services who retained the right of unrestricted game shooting in and around the reserve for tsetse control purposes. Renewed agitation for action to be taken against tsetse fly culminated in another game eradication programme which lasted from 1942 to 1950, during which period approximately 38 500 large herbivores were killed. In 1945, extensive trapping and D.D.T. spraying campaigns were undertaken in the reserve and elsewhere. These efforts finally saw the elimination of tsetse fly over large areas of its former range. In 1954 the Natal Parks Board assumed control of the game reserve, but it was not until 1956, when the boundaries of the reserve were described to the local Bantu, that people and their domestic stock were removed from the reserve. Localities of kraal sites and agricultural lands abandoned by these people are shown in Fig. 7.

It would be appropriate to summarize the history of management in the reserve since its acquisition by Natal Parks Board in this short review. However two major management decisions were of particular significance to the future biological development of the reserve. The first was implemented in 1954 and completed in 1958, when a pipe-line was extended from the Mkuze River to the Bube Pan situated approximately in the centre of the reserve, thus introducing a permanent watering point to the reserve (Fig. 1).

The second decision was implemented in 1963 when large scale animal population control programmes were initiated. Since their protection in 1954 game populations had built up rapidly until in 1961 anxiety was expressed about deteriorating veld conditions. Since then

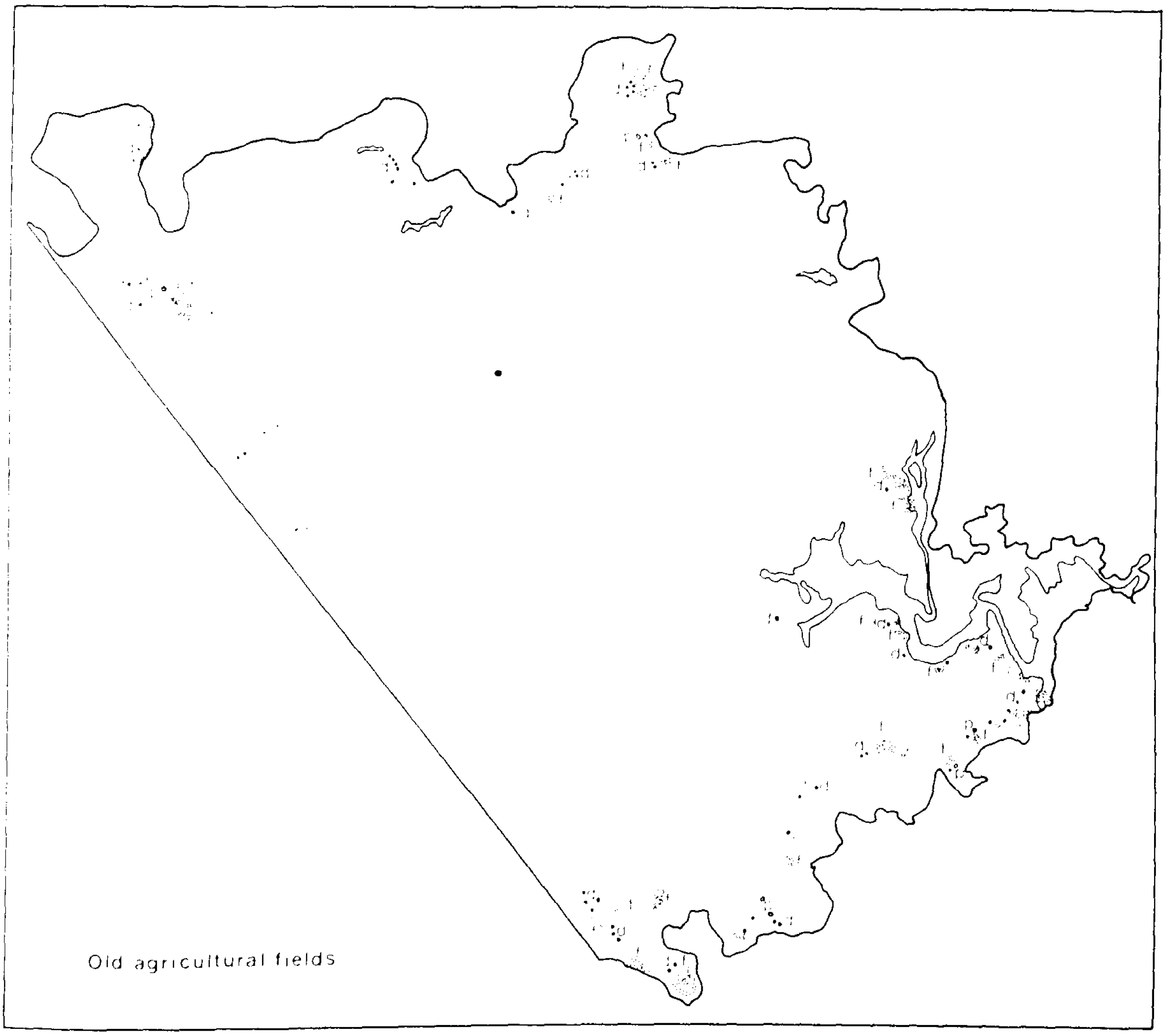


Fig. 7 Bantu dwellings(d), stock pens(p), and agricultural fields(f) as located on the 1937 aerial coverage of Mkuzi Game Reserve.

populations of 'problem' species have been controlled by regular culling. While numbers of animals removed each year have varied quite substantially, the average numbers removed over this twenty year period amount to approximately 2500 impala, 500 wildebeest, 100 warthog and 100 nyala per annum.

CHAPTER 3. LAND TYPES, SOILS AND VEGETATION

3.1 OBJECTIVES

It will be apparent from the last chapter that Mkuzi is a relatively small but complex area. Reduction in complexity, whether this is continuous or occurs as discrete units, may be achieved through classification.

The objectives of this part of the study aimed at obtaining a better understanding of the geophysical and biological complexity found in Mkuzi and were specifically:-

i) to classify, map and describe the terrain morphology and soils,

ii) to classify, map and describe the vegetation and

iii) to investigate the relationships between vegetation, site characteristics and past landuse in an effort to explain the dynamics of the area at a general level.

3.2 GENERAL APPROACH

In order to achieve the first two objectives, it was decided that an independent approach (sensu Mueller-Dombois and Ellenberg, 1974) be applied to the classification of environment and vegetation. This would then allow objective correlation between these two components as a subsequent step and in so doing, the third objective could be evaluated. An initial lack of familiarity with the soils and vegetation of the area and little previous experience in soil and vegetation classification and survey, prompted the adoption of an objective sampling strategy. The latter was chosen in preference to the selective sampling of continental phytosociological methods, which require an apprenticeship and experience for their efficient application (Bunce and Shaw, 1973; Mueller-Dombois and Ellenberg, (1974). Apart from these pragmatic reasons, however, the nature of the problem is multivariate and therefore lends itself to solution using multivariate analytical techniques which require an objective sampling strategy (Bunce and Shaw, 1973; Gauch, 1982).

The size of Mkuzi (290 km^2) and the scale of available topo-cadastral base maps and the most recent aerial photo coverage (both 1:50 000) dictated that mapping of soils and vegetation should be at a scale of 1:50 000. This corresponds to the semi-detailed (FAO : medium intensity) level of survey and as such has various implications for the intensity of sampling and the minimum size unit to be mapped, (Young, 1976; Davidson, 1980). The intensity of sampling required for the implied accuracy of a map at a specific scale (1:50 000 in this instance), and to satisfy the need for replicate sampling necessary in classification and ordination studies, depends primarily on the internal variability of individual samples and the degree of soil type or plant community variation within the study region (Mueller-Dombois and Ellenberg, 1974; Beckett and Bie, 1976; Young, 1976; Gauch, 1982).

The degree of soil type variation in a region is inherently more difficult and time consuming to estimate than is the degree of plant community variation, where aerial photo interpretation backed up by ground reconnaissance will suffice. For this reason, general guidlines exist to assist the soil surveyor in deciding on the required sample intensity (cf. Webster, 1977). Applying these guidelines to the situation in Mkuzi indicated a sample size of between 200 and 500. However, the sampling intensity required for vegetation classification and ordination calculated using the guidelines proposed by Gauch (1982), indicated that between 60 and 100 samples would be adequate.

For comparative purposes soils and vegetation data had to be collected at the same sites, and a preliminary sampling exercise indicated that 200 or more sites was in excess of the finance and time available for the project. A smaller sample would reduce the accuracy of the soil inventory and mapping, but it seemed feasible to sample approximately half this number of sites without compromising the number of samples required for vegetation community analysis and mapping. To overcome the possible deficiency in soil sample size, it was decided that where possible landtype and vegetation indicators of various soil types should be identified. These would then aid in reducing inaccuracy in the soil inventory and mapping, which results from undersampling.

While a "free" survey, or preferential sampling, in pedology and plant ecology respectively would improve sample efficiency when used by an experienced pedologist or plant ecologist, the subjective selection of sample sites may introduce appreciable bias and error in the hands of an inexperienced operator (Gauch, 1982). Of the more objective techniques necessary for the collection of quantitative data for multivariate analysis, stratified random sampling (principally accuracy and statistical validity) is more efficient than the parent strategies (Smart and Grainger, 1974; Gauch, 1982). For these reasons, stratified random sampling was adopted as the sampling framework in this study.

The final consideration with respect to the general sampling approach was that of the size and shape of the sample unit. To minimise the subjectivity involved, the species-area method (Mueller-Dombois and Ellenberg, 1974) was used to assist in the selection of an appropriate size of sample unit. The concept of minimal area in vegetation has been questioned by Kershaw (1973) and Gauch (1982), and although there is conflicting evidence, an error in the selection of sample unit size would not invalidate the results of a community analysis. The latter would seem less likely if sample plots are selected to be slightly larger than that indicated by the species-area method.

Finally, rectangular shaped sample plots were chosen as they proved to be generally more easily layed out and evaluated in the field than round or square ones. Furthermore, a rectangular plot is reputedly more efficient and representative in clumped vegetation (Gauch, 1982).

In addition to the usual soils (profile description and samples for laboratory analysis) and vegetation (community structure and species abundance) data collected in surveys of this kind, supporting environmental and historical information were collected to assist in the interpretation of the emergent soil and community patterns.

In summary, the general procedure followed for this part of the study was:

i) land type delineation, based on maps, photos and ground surveys, forming the basis for sample stratification;

ii) pilot study using 15 samples, the results of which were used to modify sample strategy, data collection and analytical methods;

iii) main data collection phase in which a further 88 sites were located and evaluated;

iv) classification and ordination of quantitative soils data;

v) a comparison of the soils and land type classifications, modifying the soils classification where necessary;

vi) classification and ordination of vegetation data;

vii) selection and evaluation of 15 "nodal" sites which in the second phase form the sites for detailed composition and structure analysis. Inclusion of these data in subsequent soil and vegetation classifications and ordinations;

viii) environmental interpretation of vegetation ordination;

ix) refinement of the vegetation classifications (physiognomic and floristic) to give mappable units using available aerial photo coverage;

x) refinement of the soil classification to allow for reliable prediction and mapping of the units, using land type and vegetation information;

xi) development of a map of vegetation physiognomic groups, vegetation communities and soil associations;

xii) use of site, soils, vegetation structure species composition data and gross changes in physiognomy to infer plant dynamics and successional relationships of plant communities.

3.3 METHODS

3.3.1 Sample strategy and field procedure

Species/area curves for trees and shrubs were determined using a system of nested quadrats at two locations in the plant community thought to have the greatest species richness, namely the Sand Veld Closed Woodland. Following this the reserve was stratified for sample site location, on i) land type, and ii) geographic coverage.

The first step located and marked the geological boundaries on aerial photographs, which were then examined under a stereoscope and the boundaries adjusted slightly to fit the apparent relief. This process resulted in delineation of the five major land types described in section 2.3. Of these the major expanse of lowlying recent alluvium along the Mkuze and Msunduzi Rivers and its associated riverine forest, woodland and floodplain grasslands, was so distinct and well delineated that it was excluded from the rest of the study.

In addition to the land type delineation, the reserve was further divided longitudinally into more or less three equal areas, which gave a total of twelve strata. Further stereoscopic analysis of aerial photographs allowed the delineation of the major vegetation boundaries within each stratum. A temporary aerial photo - mosaic was then made up and sample locations were randomly selected. Sample points were then located and marked on the photo-mosaic with the aid of a scaled down 1 km grid system drawn on transparent cellophane and placed over each stratum. The number of sample sites selected in each stratum was related roughly to the size of the stratum and to the intricacy of vegetation pattern occurring within it.

The location of each sample site in the field was aided by the use of topo-cadastral maps, the aerial mosaic, a magnetic compass and measuring wheel. On location of the site, the sample plot was orientated in such a way that the long axis ran parallel to any apparent environmental or vegetational gradient and visually checked for internal homogeneity before demarcation. If the site did not appear homogeneous, it was moved the smallest possible distance in any direction to a position that was homogeneous and data collection commenced. This is considered below under the three main headings; environmental information, geology and soils, and vegetation.

3.3.1.1 Environmental information

Environmental information included altitude (estimated to the nearest 5 m from topographical maps), slope (measured with a hand held clinometer to the nearest half degree), aspect of a sloping site (estimated as one of 16 compass sectors), and topographic situation recorded as one of the following categories; crest, waxing convex slope, midslope, alluvial foot slope and valley floor which may or may not be of alluvial origin.

Other information included evidence of:

i) damage by fire,

ii) past human occupation or agricultural activity and the nature of the evidence, and

iii) bush removal or wood cutting activities in the sample plot and for a short distance (100m) away from it.

3.3.1.2 Geology and soils

The geology of each site was determined from the geological map of the reserve and verified where possible with information gathered on site. The geological classification and map used is based mainly on stratigraphy, to a certain extent lithology and to a lesser extent the mode of occurrence of the underlying rocks. A reduced version of this map is presented in Chapter 2.3. and was derived from two unpublished sources (Bristow, 1976; Department of Geological Survey, Pietermaritzburg) and from my own ground observations.

Soil surface condition was recorded under four headings: i) rock cover, ii) the amount of bare ground, iii) the area of the plot exhibiting some form of surface sealing or capping, and iv) the type and amount of soil erosion. Characteristics i) to iii) were all estimated using the 8-point scale of Anderson and Walker (1974), while soil erosion was described by one of the following categories: o - erosion absent or very slight, 1 - slight dissection by run-off channels or gullies, 2 - erosion moderate to severe with a high percentage loss of top soil and/or marked dissection by run-off channels or gullies.

A soil profile pit 2 x 1 x 1 m deep (or to bedrock) was dug at the centre of each plot, and a profile description made according to the procedure outlined by Loxton (1963). Diagnostic horizons were identified and the soil profile classified using the South African binomial system (MacVicar *et al.*, 1977). A 1 kg disturbed sample was taken from each soil horizon for physical and chemical analysis and at 48 sites, selected to encompass the full range of soil types in the reserve, four undisturbed soil cores were collected from each horizon for determination of moisture retention properties. Finally, a Beta-auger was used to collect a 2 kg composite surface sample from the whole plot for laboratory analysis. Sample sites were regularly spaced within the plot.

3.3.1.3 Vegetation

To facilitate recording and later analysis of the data, the vegetation was divided into herbaceous, shrub and tree strata, where a species list was drawn up for the plot by two observers, the search time depending on species richness. The search was discontinued once the plot had been completely traversed by both observers and no new species had been encountered by either observer for a period of fifteen minutes. This ensured a consistant search effort and included the same proportion of species in each site.

Estimates of species cover were made at an intermediate level of accuracy, again using the scale developed by Anderson and Walker (1974), but modified slightly by adding the two lower classes of the Braun-Blanquet scale namely, "+" and "r". In addition to the cover-abundance of each species, the total cover of each stratum was estimated using this scale and finally, the modal height of each stratum was estimated in meters.

3.3.2 Laboratory analysis and data preparation

3.3.2.1 Environmental information

Information under this heading which could not be determined in the field but was nevertheless relevant included fire history and past human occupation or disturbance, including bush removal. Fire history and any bush removal programmes implemented by management were obtained from the reserve records which dated back to 1963. Past human occupation and disturbances were determined from the earliest aerial photographic coverage (1937) of the reserve. Bantu dwellings, lands and stock pen sites could be easily identified and marked on the photographs from where they were transferred to 1:50 000 base maps. Bantu occupation of the reserve ceased only in 1957 but unfortunately the more representative 1955 aerial photo coverage was not available at the time of this study.

3.3.2.2 Soils

Mechanical analysis

Surface samples collected at each site were air-dried in trays for at least a week prior to crushing. The crushed sample was then passed through a 2 mm sieve and the proportion of stones coarser than 2 mm weighed and expressed as a percentage of the total sample weight (% stone). This material was then discarded.

Water content of the air-dried sample was then determined by oven drying at 105 °C for 12 hours. Soil texture was determined using the Bouyoucos hydrometer method (Day, 1965). The proportions of clay (<0,002 mm), silt (0,002 - 0,02 mm) and sand (0,02 - 2,0 mm) were expressed as percentages corrected for the quantity of oxidisable organic matter.

Total organic carbon was estimated using two methods. Firstly, the approximate organic matter content was estimated for all samples from the weight loss on ignition for 3 hours at 4000 °C in a muffle furnace. A subsample of these samples was then analysed using the method of Waugh and Hunter (1974) and through regression analysis the organic matter content according to the Waugh and Hunter (1974) method estimated for all samples.

Chemical Analysis

A subsample from each of the samples was ground to pass through a 1mm sieve for the remaining analyses. Soil reaction (pH) was determined in normal potassium chloride using a soil to solution weight ratio of 1:2,5.

As a guide to the nutrient status of each sample exchangeable cations (calcium, magnesium, potassium and sodium) were determined individually by atomic absorption after 30 minute extraction with neutral normal ammonium acetate, using a soil to solution ratio of 1:10. Exchangeable acidity, which is related to exchangeable aluminium (M. Farina, pers. comm.), was determined by titration against sodium hydroxide after 10 minute extraction with normal potassium chloride using a soil to solution ratio of 1:10. Total exchangeable bases (T.E.B.) was calculated as the sum of exchangeable calcium, magnesium, potassium and sodium.

Phosphorus availability indices were determined using the phosphomolybdovanadate procedure (Black, 1965) after a five minute extraction with 0,05 normal sulphuric acid on a soil to solution ratio of 1:10.

Soil Moisture Characteristics

Relative soil moisture availability was determined as follows. Soil bulk density was determined on minimally disturbed profile samples extracted using the method described by Ball (1976). Samples were then brought to equilibrium on a pressure membrane apparatus at 0,05 and 15,0 mega pascals matric potential, the water contents determined and expressed as a percentage of the oven dried sample weight. The suction pressures were used as approximations of field capacity and wilting point respectively. For each sample organic matter content was determined using the method of Waugh and Hunter (1974) and particle size analysis was carried out on air-dried disturbed samples using the Bouyoucos' hydrometer method (Day, 1965). Using multiple regression analysis empirical relationships were established between clay, silt, organic matter and bulk density as independant variables, and field capacity and wilting point as dependant variables for the topsoil. Using the same independant variables, but excluding organic matter, similar relationships were established for the subsoil. Using these relationships, estimates of field capacity and wilting point were then obtained for the remaining unsampled sites.

For the purposes of the multivariate analysis all the above variables, excluding those concerned with moisture availability were stored in a full format matrix (Gauch, 1977) on computer file. These variables included surface rock cover, A horizon grit, clay, silt, sand, pH, organic matter, phosphorus, calcium, magnesium, potassium, sodium, aluminium, total exchangeable bases (T.E.B.), T.E.B. per 100 g clay, B-horizon stones, clay, silt and the profile depth.

3.3.2.3 Vegetation

Complete herb, shrub and tree species lists were constructed from individual field sheets. In all there were 370 herbaceous (96 graminaceous herbs and 274 forbs), 162 shrubs and 66 tree species. Every species from each list was then assigned a number, in alphabetical order. Each field sheet was then coded according to these numbering systems and at the same time cover-abundance values were converted to their equivalents in per cent (Anderson and Walker, 1974), with both "+" and "r" being allocated the lowest percentage value of one.

3.3.3 Data analysis

3.3.3.1 Multivariate techniques

The recent proliferation of multivariate techniques has created a dilemma for ecologists. Very often experimentation with a number of different techniques is resorted to with the danger that the original biological problem becomes of secondary importance to a study of multivariate methods.

The fact that each data set has its own character (i.e. attribute response curves, noise, redundancy and outliers - Gauch, 1982), mitigates against there being a single "best approach" and further adds to the complexity of the problem. However, decision trees such as those found in Goldsmith and Harrison (1976) and Jeffers (1978) can assist greatly in the choice of an analytical strategy, and recently comparative evaluations of various ordination techniques (Austin, 1976; Kessel and Whittaker, 1976; Gauch and Wentworth, 1976; Gauch, Whittaker and Wentworth, 1977; Fasham, 1977; Hill and Gauch, 1980) have improved understanding and application of many of these. Similarly the texts by Sneath and Sokal (1973), Williams (1976) and more recently that by Gauch (1982) have summarised much information on, and make recommendations for, the use of the multitude of classification techniques available.

Several principles which are relevant to the selection of appropriate multivariate techniques have emerged (Gauch, 1982). The method selected should:-

1) be effective in summarizing the variation in the data set and should therefore be (a) realistic in their assumptions about

the structure of the data and (b) the summarized information should be easily conveyed to the user,

2) be robust in that they should perform well on a wide variety of data sets and
3) be economical to execute and have "only ordinary demands on the investigator's time and expertise" (Gauch 1982).
4) Different techniques are likely to highlight different aspects of the data. To gain a better insight into the properties of the data set it is therefore desirable to undertake analyses using a few different methods and to compare results (Williams, 1976; Pielou, 1977; Webster, 1977; Gauch, 1982).

With the first three criteria in mind, Gauch (1982) recommends the use of detrended correspondence analysis (Hill, 1979a) above all other indirect gradient analysis techniques but further comments that in cases of low sample heterogeneity, principal components analysis is better for analysing plant community data. For large data sets (more than 100 samples) he finds non hierarchical classification, for example composite clustering (Gauch, 1979), useful for preliminary summarization of redundancy, reducing noise and indentifying outliers. For smaller data sets (less than 100 samples) several authors (Williams, 1976; Pielou, 1977; Webster, 1977; Gauch, 1982) have favoured a divisive polythetic strategy as being the ideal hierarchical classification system. Two-way indicator species analysis (Hill, 1979b) was developed with this ideal in mind and Gauch (1982) suggests that this is the most robust and effective divisive polythetic technique available at present

With the exception of composite clustering, which was not available at the time of analysis, all the techniques mentioned above were used in the analysis of both soil and vegetation data collected in this study. In addition, Orloci's (1967) sums of squares method, an agglomerative, polythetic, hierarchical clustering technique was used for comparison with the results obtained from two way indicator species analysis. Furthermore, as hierarchical classification is not altogether appropriate for the analysis of soils data (no soil population studied so far has been shown to possess hierarchical structure (Webster, 1977)), canonical variates analysis was used as a "hybrid" non-hierarchical classification routine.

Descriptions of the multivariate methods used are covered in detail in the literature so only a brief description of each is given below.

Principal component analysis

Principal component analysis is the oldest, the simplest and probably the best known of the multivariate models. It has been applied in one form or another on numerous occasions in both pedological and biological contexts and has now been described in a large number of biologically orientated texts (Seal, 1964; Gittins, 1969; Williams, 1976; Pielou, 1977; Webster, 1977; Jeffers, 1978; Gauch, 1982, to name a few).

The primary purpose of principal component analysis (and that of other indirect gradient analysis techniques) is to bring about a reduction in the dimensionality of data from extremely high (equal to the number of samples or the number of variates) in the raw state, to low, normally in the order of one to three dimensions. Furthermore, this reduction in dimensionality must be accomplished in such a way that none of the important features of the pattern residing in the original data are lost.

Principal component analysis achieves this reduction in dimensionality by transforming a given set of variates into a new set of composite variates or principal components that are orthogonal to each other. The first principal component represents the best linear combination of the original variates, where best is defined by minimizing the squared perpendicular distance between the variates and the component. The first principal component therefore may be viewed as the best summmary of a linear relationship exhibited by the data and thus singularly accounts for the largest amount of variance in the data. The second component is defined as the second best linear combination of variates which accounts for the largest amount of residual variance after the effect of the first component is removed from the data, and for this reason it is orthogonal to the first. Subsequent components are defined until all the variance in the data is exhausted. Unless one variate is perfectly correlated to one or a combination of the rest of the variates in the data, the principal component solution requires as many components as there are variates.

Since each successive component extracts the maximum amount of residual variance, successful data reduction occurs when the first few components explain most of the variance in the data. In this instance, the lower dimensional projection of the data points allows an easier insight into the apparent structure residing in the cloud of points representing the data set.

Two important points emerge, namely:

1) The magnitude of variance that is extracted by any component may have no bearing on the pedological or ecological meaning or validity of the projection of points defined by that component. Assessment of results can only be in terms of the insight afforded by the analysis,
2) The principal component model assumes linearity of response of the variates to each component. This is clearly an unrealistic assumption when considering the response of species to environmental gradients, which is typically unimodal, but may also be bimodal (Greig-Smith, 1980). In the instance where species show bell-shaped response curves along an environmental gradient, this gradient will be recovered not in a linear form, but commonly distorted into an arch thus making interpretation difficult (Swan, 1970; Gauch, 1982). In the analysis of vegetation data this may be overcome to a certain extent by limitiang the length of the gadient analysed to one of low beta-diversity. Simply put, this means that most stands in the sample will contain most of the species, but in different amounts and as a result, there would be few zero values in the raw data matrix. While this weakness of the principal component model in the analysis of vegetation data is realized, soil attributes often do show uni-directional if not strictly linear response curves and hence principal component analysis would seem quite appropriate for the reduction of soils data (Williams, 1976).

Detrended Correspondence Analysis

Detrended correspondence analysis (Hill, 1979a; Hill and Gauch, 1980; Gauch, 1982) is an indirect gradient analysis technique based on, but substantially improving, an associated technique called reciprocal averaging (Hill, 1973; Gauch, 1982). Reciprocal averaging is solved computationally in a similar way to principal component analysis, but is conceptually related to the weighted averages technique of Curtis and McIntosh (1951). In contrast to principal component analysis, reciprocal averaging ordinates samples and species simultaneously by iteration in which weighted averages are used to calculate sample scores from species scores and vice versa. To start the first iteration species scores are initially arbitrarily assigned. In the second iteration, new species scores are calculated by weighted averages from the sample scores and the process continues until the scores stabilize, converging to a unique solution which is unrelated to the initially assigned species scores. This represents the first reciprocal averaging axis. After correcting for this axis, a second axis may be extracted by the same iterative method, which may then be followed by the extraction of a third axis after correcting for the first two. As in principal component analysis, the amount of variance extracted by each successive axis diminishes.

Despite the fact that reciprocal averaging performs better than principal components analysis on heterogeneous data sets with long gradients, it still has two major faults.

1) The second axis may be a quadratic distortion of the first axis i.e. the arch problem encountered in principal components analysis
2) The ends of the first axis are compressed relative to the middle. Thus the separation distances in the ordination do not carry a consistant meaning in terms of implied differrences between the objects being ordinated (Gauch, 1982).

Detrended correspondence analysis was designed to correct the two major faults found in reciprocal averaging by the process of detrending. Detrending involves the subdivision of the first axis into a number of segments and within each segment the scores on the second axis are adjusted to an average of zero. This process is