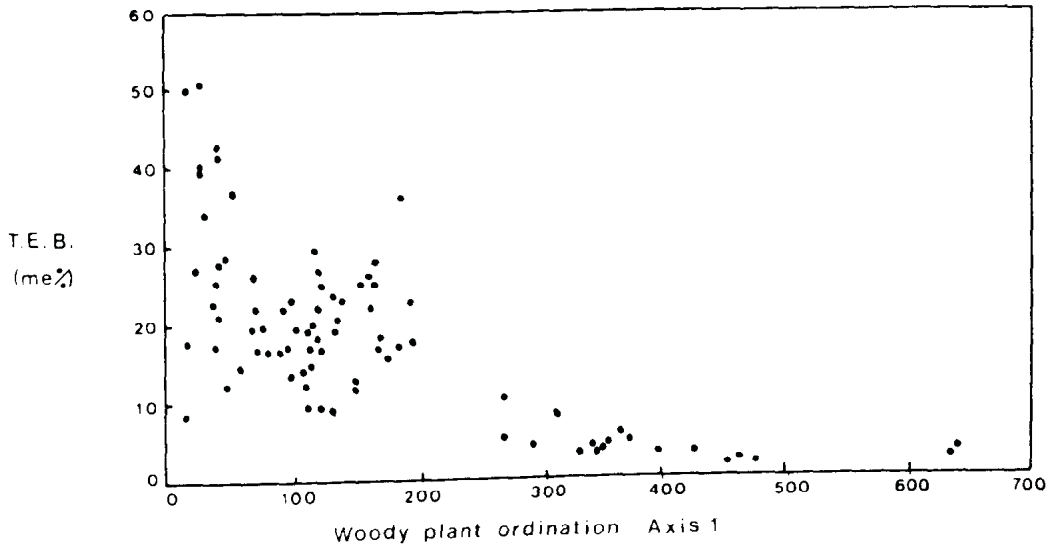


Fig. 18d Relation between total exchangeable bases (T.E.B.) and sample position on the first woody plant ordination axis.

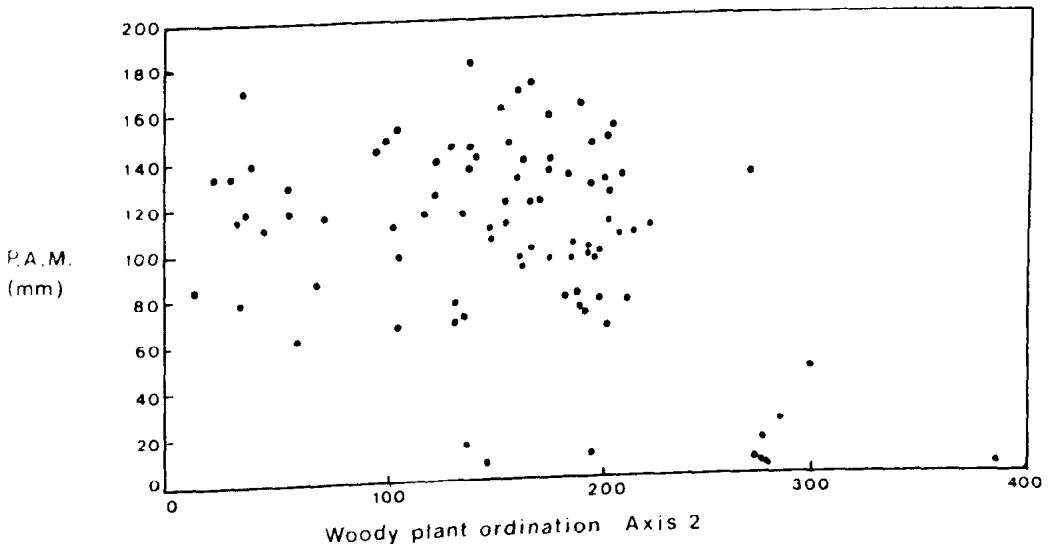


Fig. 18e Relation between profile available moisture (P.A.M.) and the second woody plant ordination axis.

closely related and thus the latter resemblance is not unexpected. However, at a total exchangeable base level of approximately 5 me% and greater, most soils in Fig. 18d are base saturated. Although there might appear to be a fairly marked relationship between exchangeable bases and this axis, the relationship with available nutrients is much less evident.

To summarise this first axis then, it would appear that no single environmental factor can explain the variation along it and thus it would appear to be a complex gradient involving both moisture and nutrient availability. The plot of profile available moisture vs. stand position on the second vegetation axis was the only relation to show a consistent trend with regard to this axis (Fig. 18e). The lithosols and lithic soils occur high on the vegetation axis and low on the profile available moisture axis. The data points are however fairly widely scattered. This scatter could be considerably reduced if the effects of rooting depth, water run-on and run-off, aspect and the occurrence of an underground or perched water table could be accounted for. It seems likely then that the second vegetation ordination axis is most probably related to moisture regime.

3.4.2.3.3 Herbaceous layer ordination and environmental interpretation

The first two axes extracted by the detrended correspondence analysis of the herbaceous data show two fairly clear gradients (Fig. 19). The first axis which has a gradient length of 5,998 half changes has species characteristic of the taller coarse grasslands of the Lebombo foothills (*Andropogon gayanus, Trachypogon spicatus, Setaria perennis*, and *Cymbopobgon excavatus*) at its positive extreme and species characteristic of low lying, base rich, black clay soils (*Enteropogon monostachyus, Rhytachne latifolia*) and a species characteristic of moderately leached yellow brown sands (*Eragrostis pallens*) sharing the negative extreme (Fig. 19).

The second axis with a gradient length of 4,190 half changes, separates the plants found on the two soil types mentioned above into species characteristic of the moderately leached yellow brown sands (*Eragrostis pallens, Digitaria longiflora, Sacciolepis curvata, Aristida congesta* subsp. *congesta*) at the positive extreme, from the

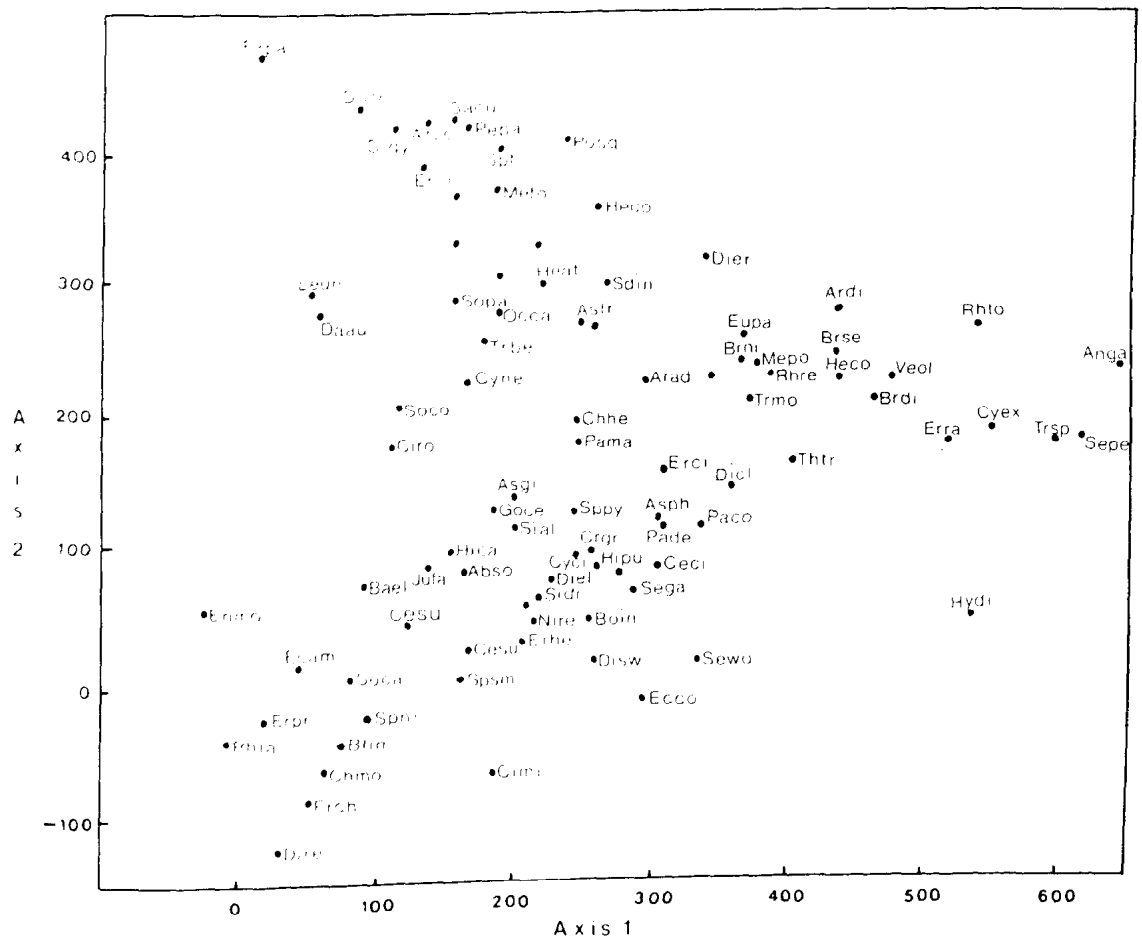


Fig. 19 Detrended correspondence analysis of edited herbaceous data matrix. Selected species plotted in the space defined by the first two ordination axes. See Table 4 for names to species abbreviations.

species of lowlying sometimes flooded base rich black clay soils (*Dinebra retroflexa*, *Eragrostis chloromelas*, *Cienfuegosia hildebrandtii* (forb), *Chloris mossambicensis*, *Blepharis integrifolia* (forb) and *Rhytachne latifolia*) at the negative extreme (Fig. 19).

Table 4. Herbaceous plant names and abbreviations used in figures. Nomenclature is according to Ross (1972). Changes in grass names given by Gibbs-Russel and Smook (1980), are accepted here.

Grasses

Abbr.	Name	Abbr.	Name
Anga	Andropogon gayanus	Arad	Aristida adscensionis
Arba	A. congesta subsp. barbicollis	Arco	A. congesta subsp. congesta
Ardi	A. diffusa	Boin	Bothriochloa insculpta
Brdi	Brachiaria dictyoneura	Brni	B. nigropedata
Brse	B. serrata	Brxa	B. xantholeuca
Ceci	Cenchrus ciliaris	Chmo	Chloris mossambicensis
Chvi	C. virgata	Cyex	Cymbopogon excavatus
Daau	Dactyloctenium australe	Digy	Digitaria gymnostachys
Dier	D. eriantha	Dilo	D. longiflora
Disw	D. Swazilandensis	Dire	Dinebra retroflexa
Diel	Diplachne eleusine	Ecco	Echinochloa colonum
Ence	Enneapogon cenchroides	Enmo	Enteropogon monostachyos
Erch	Eragrostis chloromelas	Erci	E. cilianensis
Ercl	E. ciliaris	Erhe	E. heteromera
Erpa	E. pallens	Erra	E. racemosa
Erri	E. rigidior	Ersu	E. superba
Erpr	Eriochloa parvispiculata	Eupa	Eustachys paspaloides
Heco	Heteropogon contortus	Hydi	Hyperthelia dissoluta
Leun	Leptochloa uniflora	Paco	Panicum coloratum
Pade	P. deustum	Pama	P. maximum
Pepa	Perotis patens	Posq	Pogonarthria squarrosa

Table 4 cont.

Abbr.	Name	Abbr.	Name
Rhru	Rhynchelytrum repens	Rhla	Rhytachne latifolia
Sacu	Sacciolepis curvata	Sega	Sehima galpinii
Sepe	Setaria perennis	Sewo	Setaria woodii
Spfi	Sporobolus fimbriatus	Spni	S. nitens
Sppy	S. pyramidalis	Spsm	S. smutsii
Thtr	Themeda triandra	Trsp	Trachypogon spicatus
Trbe	Tragus berteronianus	Trmo	Trichilaena monachne
Trgr	Trichoneura grandiglumis	Urmo	Urochloa mosambicensis

Forbs

Abbr.	Name	Abbr.	Name
Abau	Abutilon austro-africanum	Abso	A. sonneratianum
Acas	Achyranthes aspera	Asfr	Asclepias fruticosa
Asph	A. physocarpa	Asgy	Asystasia gangetica
Bael	Barleria elegans	Blin	Blepharis integrifolia
Cesu	Centema subfusca	Chhe	Chascanum hederaceum
Cihi	Cienfuegosia hildebrandtii	Ciro	Cissus rotundifolia
Crgr	Crossandra greenstockii	Cyci	Cyphostemma cirrhosum
Dicl	Dicliptera clinopodia	Ecam	Ecbolium amplexicaule
Goce	Gomphrena celosiodes	Heat	Helichrysum athrixiifolium
Heca	Hermbstaedtia caffra	Hica	Hibiscus calyphyllus
Hipu	Hibiscus pusillus	Jufl	Justicia flava
Mefo	Melhania forbesii	Mepo	Melhania polygama
Nire	Nidorella resedifolia	Occa	Ocimum canum
Rhto	Rhynchosia totta	Sial	Sida alba
Sidr	S. dregei	Soca	Solanum capense
Soco	S. coccineum	Soin	S. incanum
Sopa	S. panduraeforme	Thdr	Thunbergia dregeana
Veol	Vernonia oligocephala		

This second axis can be described with some confidence as a gradient from free draining, moderately leached sandy soils to poorly drained, base rich clays in bottom lands. It is more difficult, however, to give a meaningful environmental interpretation to the first axis, mainly because of the large differences in environmental conditions under which the end point species grow. The species at the positive end of the first axis are characterised by growing on rocky soils with relatively steep slopes, a relatively sparse woody plant cover and frequent occurrence of fire (every 3-5 years). By contrast, the species at the negative end of this axis grow on either sands or clayey, non-rocky soils, relatively flat slopes, a high woody plant cover in the form of closed woodland or thicket and seldom, if ever, support fire.

The third and fourth axes appear relatively important with gradient lengths of 2,769 and 2,55 half changes respectively, but are extremely difficult to interpret. The third axis has species characteristic of the base rich black clays (*Dinebra retroflex, Eragrostis chloromelas, Chloris mossambicensis, Echinochloa colona, Rhytachne latifolia*) at its positive extreme and species associated with heavy grazing pressure (*Trichoneura grandiglumis, Blepharis integrifolia, Chloris virgata, Sporobolus nitens, Aristida adscensionis, Rhynchelytrum repens, Aristida congesta* subsp. *barbicollis*) or extremely skeletal substrates (*Aristida diffusa, Tricholaena monachne*) at the negative extreme. So that while this gradient appears associated with disturbance, it still has a strong element of association with the physical environment. Assuming that grossly different environments have different species characterizing their late successional and pioneer (disturbance) end points, to fully elucidate these successional relations it would be necessary to subdivide the data into groups of more or less similar environment and then analyse these groups separately. The fourth axis is largely uninterpretable.

To summarize, the herbaceous vegetation appears largely influenced by the same environmental gradients as the woody vegetation. These are: 1) a gradient from high lying well drained rocky soils of the Lebombo foothills where the herbaceous community is lightly grazed and frequently burnt, to the lower lying situations on rock free sands or

clays of the coastal flats where the herbaceous community is grazed more heavily and seldom experiences fire, 2) a gradient from sandy well drained moderately leached soils, to heavy black base rich clays which at the extreme become waterlogged at times during the rainy season, and 3) a weak gradient associated with disturbance but largely being masked by strong associations with the physical environment.

3.4.2.3.4 Vegetation classification and environmental characterization of groups

The vegetation classification derived here is orientated towards mappable communities. Since at a scale of 1:50 000 it is only feasible to map woody communities, no attempt has been made to integrate a formal herbaceous classification with the woody plant classification. Instead the herbaceous data from each woody community are summarized and presented with the woody plant and environmental summaries for that community . On a few occasions the herbaceous characteristics of a sample have helped allocation of samples to vegetation types.

The cluster analyses of the woody plant data using the divisive two-way indicator species analysis and Orloci's agglomerative technique, have resulted in similar sample groupings, but in general the overall structure of the hierarchies is different. Theoretically the divisive technique ought to have better structure at the upper levels of the hierarchy and the agglomerative technique ought to have tighter and more viable groups at the lower levels. This is upheld by the two classifications of these data. The divisive technique separates plant associations found on the deeper sandy soils as a single large group from the rest of the samples at the first division in the data set and the associations characteristic of the shallow rocky soils of the Lebombo Mountains are separated as a second large group at the next level of division (Fig. 20a). By contrast, the agglomerative classification shows very little of this overall hierarchical structure. For example, the two major associations on

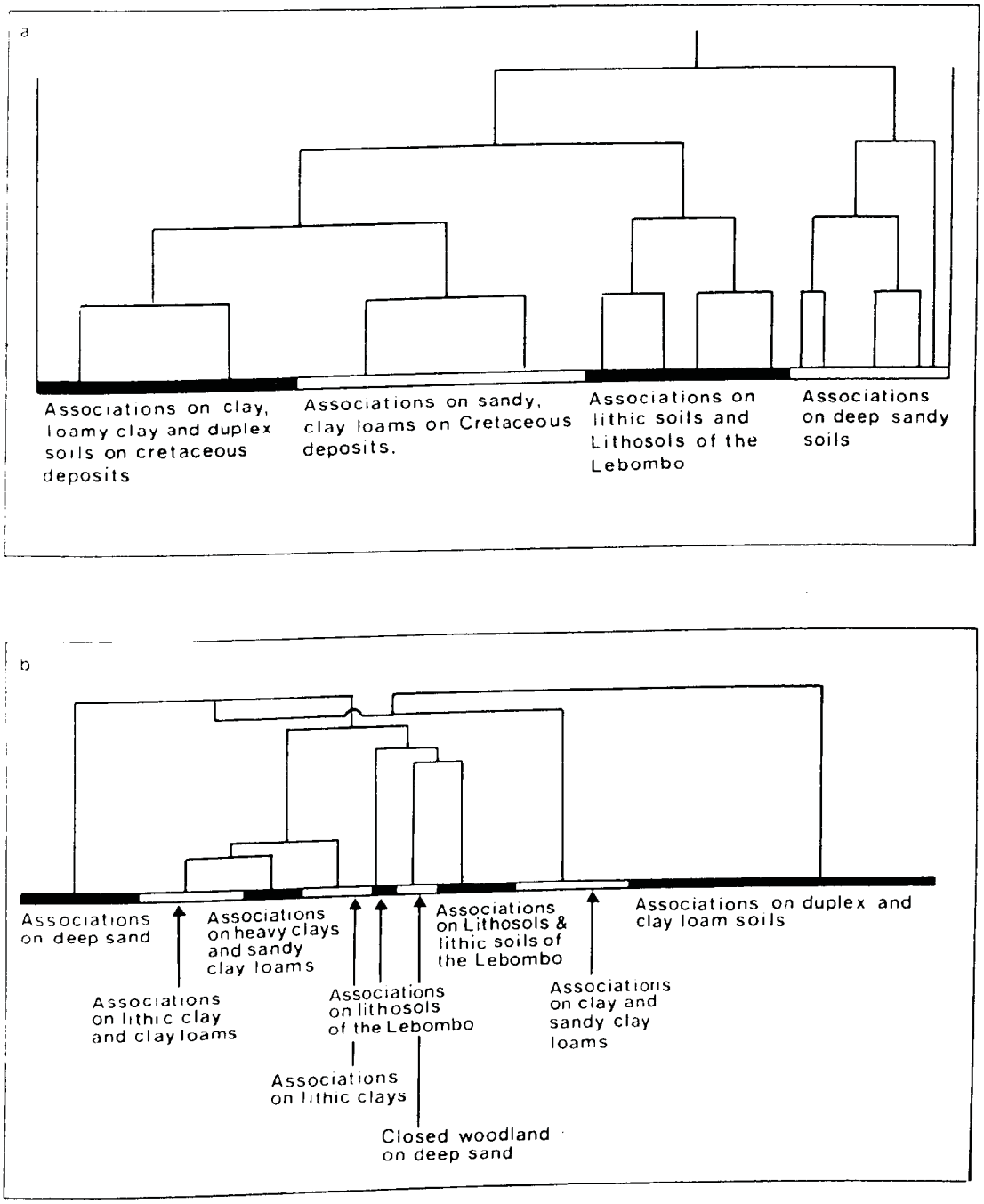


Fig. 20 The higher levels of subdivision resulting from the application of a) divisive two-way indicator species analysis and b) Orloci's agglomerative technique, to the combined woody plant data.

sand, although reproduced faithfully in the classification, are not joined until the final stages of the agglomeration procedure (Fig. 20b). Similarly, the associations characteristically found on the shallow soils of the Lebombo foothills are not joined in the same major hierarchy at all (Fig. 20a and 20b).

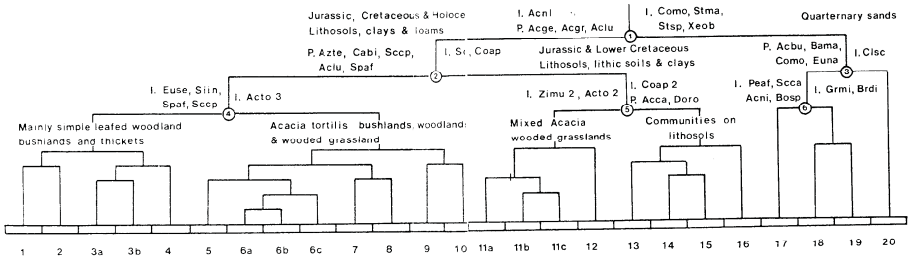
The final classification is derived from both cluster analyses using the results of the two-way indicator species analysis as the overall hierarchical framework of the classification and the results of the agglomerative analysis and environmental characteristics to help place individual samples correctly in their respective groups. The main features of this classification are condensed into Fig. 21. Only the first six divisions and their floristic indicators are considered in some detail below.

Division 1 (Fig. 21)

At this level, vegetation types associated with the Quarternary sand deposits (types 17 - 20) are separated from those found on soils with a finer texture, high base status, impeded drainage and which are derived from volcanic and marine sedimentary deposits. Floristic indicators of this division are *Combretum molle, Strychnos madagascariensis, Strychnos spinosa* and *Xeromphis obovata* associated with sands, and *Acacia nilotica* an indicator and *Acacia gerrardii, Acacia grandicornuta* and *Acacia luederitzii* preferential for soils derived from volcanic and cretaceous sedimentary rocks (Fig. 21).

Division 2

The second division separates vegetation types associated with rocky generally shallow soils (derived from volcanic rocks), from the types associated with finer textured soils derived from Lower and Upper Cretaceous sediments. Floristic indicators of this division are *Sclerocarya caffra* and *Combretum apiculatum* associated with the lithic soils and *Azima tetracantha, Carissa bispinosa, Schotia capitata, Acacia luederitzii* and *Spirostachys africana* showing strong preference for the non-rocky finer textured soils (Fig. 21). The major geomorphic regions of the reserve are therefore separated in the first two divisions of the classification.



Vegetation type	1	2	3a	3b	4	5	6a	6b	6c	7	8	9	10	11a	11b	11c	12	13	14	15	16	17	18	19	20
Physiognomy	Bbss	Wse	Bblc	Sss	Bts	Bblc Btc	Wlc Bblc	Slc	Slc	Wlc Bblc	Wlc Slc	Ssc	Slc	Ssc	Ssc	Ssc	Ssc Slc	Wlc	Bbsc	G	Sss	Wss Sss	Wss Bbss	Bbss Sss	Fss Bbss
Floristic Trees	Spaf	Acgr	Acnl	Siin	Bosp	Aclu	Acnl	Acto	Spaf	Acto	Acto	Acto	Acto	Spaf	Acto	Acnl	Acnl	Acka	Doro	Fiso	Coap	Como	Tese	Ptmy	Clsc
	Siin	Spaf	Spaf	Zimu	Acnl	Eudi	Aclu	Acnl	Acni	Acnl	Acse	Acni	Acg	Acni	Zimu	Acni	Acto	Scca	Acnl	-	Ozob	Acbu	Zimu	Stsp	Hyul
	Eudi	Eusc	Siin	Acka	-	Acnl	Acto	Spaf	Acto	Eudi	Acnl	Bosp	Acn	Acbu	Acni	Zimu	Acni	Acge	Scca	-	Scca	Zimu	Ptmy	Boal	Crgr
	Eusc	Siin	Beze	Paca	-	Acse	Acgr	Alan	Acse	-	-	Acge	Acn	Acni	-	Aclu	Coap	Acni	Zimu	-	-	Bosp	Achu	-	Ptmy
Shrubs	Aclu	Aclu	Aclu	Aclu	Eudi	Aclu	Aclu	Eudi	Dici	Cate	Azte	Dici	Eudi	Alan	Eudi	Eudi	Dici	Doro	Hena	Dily	Dici	Rhgu	Xeob	Ptmy	Crps
	Cabi	Mase	Ehri	Ehri	Acgr	Dici	Eudi	Mase	Cana	Mase	Ehri	Mase	Dici	Dici	Mase	Grmo	Mahe	Dici	Mahe	Mahe	Acni	Grbi	Stma	Stma	Sale
	Sccp	Rhgu	Eudi	Eudi	Aclu	Grca	Cabi	Saan	Eudi	Dici	Cana	Acse	Zimu	Ehri	Rhgu	Dici	Ehri	Alma	Acca	Alma	Acni	Grca	Euna	Brdi	Crst
	-	-	Grca	Insc	Ehri	Mase	Mase	Dici	Maed	Zimu	Dici	Eudi	-	Siin	-	Ehri	-	Mahe	Grmo	Plam	Zimu	Stma	Rhgu	Cate	Rhtr
Grasses	Enmo	Daau	Enmo	Thtr	Enmo	Erri	Daau	Daau	Spni	Pama	Pama	Ersu	Boin	Pama	Thtr	Thtr	Thtr	Thtr	Thtr	Cyex	Thtr	Daau	Spfi	Erpa	Digy
	Daau	Pama	Erch	Sewo	Spni	Chmo	Enmo	Spni	Arba	Thtr	Urmo	Arba	Disw	Chga	Pama	Boin	Pama	Anga	Pade	Thtr	Heco	Spfi	Daau	Arco	Pade
	Pade	Spni	Pama	Pama	Daau	Daau	Spni	Arba	Enmo	Daau	Daau	Erri	Pam	Paco	Pade	Pama	Trmo	Pade	Arba	Heco	Dier	Pama	Dier	Spfi	Pama
	Pama	Enmo	Chmo	Boin	Pama	Pama	Pama	Enmo	Erri	Cysp	Spfi	Thtr	Thtr	Thtr	Paco	Arba	Arba	Pama	Dier	Erra	Ardi	Arco	Arco	Dier	Sacu
Environment																									
Geology	Cr_2Cr_3	Pl/Cr_2	Cr_3	Cr_3/J	Cr_2	Cr_2Cr_3	Cr_2Cr_3	Cr_2	Cr_3	Cr_2	Cr_2	Cr_2Cr_3	Cr_3	Cr_3J	H	H/J	J	J	J	J	J	Pl	Pl	Pl	Pl
Landscape position	F	M	LM	LM	F	LM	LM	LM	C	LM	LM	C	M	C	F	F	M/LM	M	C	C	C	M	M	LM	UM
Slope	0,5	2,1	1,0	1,1	3	0,7	0,5	0	0,9	0,5	1,0	1,8	2,8	1,3	0,4	0,5	3,4	7,6	13,8	15	5,6	1,8	2,4	0	5,0
Soils																									
Rock cover	0,5	0	2,5	1	1,7	1	0	0	0,5	0	0	0	3	0,5	0,2	3,2	24	50	62	82	53	0	0	0	0
Clay A	34,6	9,6	51,0	40,5	31,0	10-61	34-3	37	23,5	26,7	28,6	29,9	46,6	34,5	30,8	36,0	26,3	32,6	35	37	24,5	11,8	7,9	8,0	10,5
Silt A	11,6	3,8	16,0	14	15,0	2-16	15,5	11,3	8	7,8	15,0	7,7	12,7	16,5	16,5	16,3	9,8	13,4	24	20	14,8	2,5	2,1	2,0	1,0
Sand A	53,8	85,4	33,0	45	53,3	21-85	49,8	51,3	68,5	65,5	56,2	61,7	39,3	49	55,3	45,5	64	54	41	42	60,5	85,2	88,4	89,5	88
pH	5,7	5,7	6,3	5,4	6,2	4,8-5,6	5,6	5	5,0	4,9	5,1	5,2	4,9	5,1	5,2	5,1	5,4	5,2	5,9	4,1	5,3	5,2	4,7	4,0	3,8
OM	2,5	1,2	3,4	2,8	1,9	0,7-23	2,3	2,0	1,2	1,5	2,1	1,6	3,2	3,1	2,9	3,2	2,8	3,8	5,5	3,4	3,1	0,8	0,58	0,35	0,75
P(ppm)	4,9	6,4	1,7	3,6	2,7	1-5	2,9	16,7	18,0	2,6	26,1	4,7	1,2	6,3	5,0	7,0	7,4	8,4	16,7	4,9	6,2	2,0	3,4	1,6	0,1
T.E.B.($me^+_/_0$)	24,0	9,6	42,2	18,7	30,2	5-37	19,4	10,4	25,3	10,1	14,8	10,0	18,4	24,7	16,9	20,9	18,8	20,7	32,2	10,5	15,7	4,8	3,4	0,98	2,0
Al($me^+_/_0$)	0,02	0,02	0,04	0,02	0,03	0,01-0,04	0,05	0,04	0,01	0,04	0,06	0,03	0,04	0,01	0,01	0,01	0,03	0,02	0,03	0,02	0,02	0,03	0,12	0,82	0,91
Stones B	7,1	0	18,8	35,0	8,3	0-60	11,3	1,7	30,0	4,2	6,0	0,7	2,1	42,5	11,3	51,7	75	72	80	95	89	0	0	0	0
Depth (cm)	>100	>100	>100	>100	>100	>100	>100	>100	>100	>100	>100	99	79	85	>100	80	40	50	45	20	21	>100	>100	>100	>100
P.A.M.(mm)	132,8	81	130	103	135	69-181	121	143	121	105	120	131	100	100	121	65	33	33	26	8	10	90	98	83	85

Fig. 21 Hierarchical classification of the vegetation of Mkuzi with phyiognomic, floristic and environmental summaries. Indicator(I) and preferential (P) species indicated on the dendrogram are those extracted by two-way indicator species analysis.

① - division number. Names for species abbreviations may be found in Tables 2 (woody plants) and 3 (herbaceous plants). Physiognomic abbreviations are:- F - Forest, Bb - Bushland, Bt - Thicket, W - Woodland, S - Wooded grassland, G - Grassland. Height classes are:- l - low, s - short. Leaf types are:- s - simple, c - compound.

For geological abbreviation see Fig. 5. Landscape position abbreviations are:- C - Crestslope, UM - Upper Midslope, M - Midslope, LM - Lower Midslope, F - Footslope or Bottomland.

Division 3

Here the major vegetation associations on sand are divided into a fairly distinct type consisting of short, simple leafed forest, closed woodland and bushland on acid sands indicated by the presence of *Cleistanthus schlechteri* on the one hand, (type 20) and on the other, wooded grasslands, woodlands, and bushlands on sand (types 17, 18 and 19) which have *Acacia burkei, Balanites maughamii, Combretum molle* and *Euclea natalensis* as preferentials (Fig. 21).

Division 4

At this level the vegetation associations on Cretaceous deposits are divided into a group (types 1 - 4) consisting primarily of simple and compound leafed semi-deciduous bushlands and thickets with *Euclea schimperi, Sideroxylon inerme, Spirostachys africana* and *Schotia capitata* as indicators, and a large group of primarily compound leafed bushlands, woodlands and wooded grasslands with a moderate (10 - 25%) cover abundance of *Acacia tortilis* as the indicator species. Both these groups are associated with relatively flat topography (maximum slope c. 3°) but the former is primarily associated with footslope and lower midslope landscape positions (areas of water run on) while the latter is associated with crestslope, midslope and lower midslope landscape positions (areas of water run on and run off). This would seem to indicate that amongst other things, micro-relief may be important in influencing the floristic changes which brought about this division (Fig. 21).

Division 5

Here the associations on soils derived from volcanic rocks and associated Lower Cretaceous sediments are subdivided into a group (types 11 and 12) consisting primarily of short, compound leafed wooded grasslands on shallow lithic clays and sandy clay loams derived from Cretaceous sediments, and a group (types 13 - 16) with variable physiognomy but all occurring on fairly shallow Lithosols. This division is characterised by *Acacia tortilis* and *Ziziphus mucronata* (cover-abundance 2-12%) as indicators of the mixed Acacia wooded grasslands on the lithic clays and sandy clay loams and *Combretum apiculatum* (cover-abundance 2-12%) as an indicator and *Acacia caffra*

and *Dombeya rotundifolia* as preferential species for the vegetation types on lithosols (Fig. 21).

Division 6

This division separates the woodlands, bushlands and wooded grasslands on sands into a distinct type (type 17), the *Combretum molle* woodland and wooded grassland on red base rich sands (ferruginous arenosols) with *Peltophorum africanum, Sclerocarya caffra, Acacia nigrescens* and *Bolusanthus speciosus* as indicators, and a group consisting two types (18 and 19) found on acid sands which are not fully base saturated. The latter group has *Grewia microthyrsa* and *Brachylaena discolor* as its indicators. At the next level this group is split into two; a *Terminalia/Ziziphus* woodland and bushland (type 18) with slightly higher base saturation than *Pteleopsis/Strychnos* bushland, and wooded grassland having *Croton gratissimus* as the indicator species. *Acacia burkei, Combretum molle* and *Euclea natalensis* are preferential species for the *Terminalia/Ziziphus* woodland and bushland.

3.5 DISCUSSION

3.5.1 Methods

3.5.1.1 Approach, sample strategy and data collection

The general approach and sample procedure was appropriate, efficient and easy in its application. The information derived from each sample site was collected in an objective and standardized manner, the vast majority of which was used in either analysis or interpretation of the results.

During the initial phases of data analysis some sample sites appeared to be inconsistent with the general pattern when comparing their soil and biological affinities. Re-examination of these sites, indicated that these inconsistencies could in nearly all cases be explained by heterogeneity in the site caused by non-uniform soil conditions (eg. termite mounds) or past disturbance. Since the relative proportion of these sites was small (<5%), they are thought to have had little effect on the final interpretation of the multivariate analyses undertaken.

The sampling of the environmental factors which were used to interpret gradients of vegetation change may also be subject to some criticism. In this respect the collection of a composite soil sample which gives a better average condition over a whole site was only made from surface horizons, subsoil samples being restricted to the profile pit within each sample site. With the limited finance available it was decided to analyse only the surface samples, and in retrospect it seems to have consistently misplaced only the duplex soils.

A second shortfall was the incomplete record of past disturbance. A major deficit is the lack of aerial photos at the time the majority of the local population abandoned the reserve. While this would locate the most recently abandoned dwellings and agricultural lands, it would still not help overcome the shortfall in our knowledge of the past grazing and burning regimes. Furthermore, the past presence of Stone and Iron Age Man is well known in Mkuzi and the possible extent of their impact on the landscape has been documented by a number of

authors for other areas (Hall, 1979 and 1980; Feely, 1980). As yet very little is known of the effect these people might have had on the vegetation dynamics of Mkuzi.

3.5.1.2 Analytical techniques

Of the wide range of analytical techniques used in the main body of the analysis, prinicipal component analysis has been extensively used and is well understood; Orloci's sums of squares methods is considered to be one of the better agglomerative clustering routines (Pielou, 1977); two-way indicator species analysis is considered superior to other forms of hierarchical clustering (Gauch, 1982) and detrended correspondence analysis is considered more robust than any other ordination technique for analysing vegetation data (Hill and Gauch, 1980). Furthermore these techniques have been used in a largely complementary fashion throughout the study.

Two criticisms may be levelled at the analysis undertaken thus far. Firstly, the soils and vegetation were ordinated using two different techniques namely principal component analysis and detrended correspondence analysis respectively, and the resulting gradients compared. The reason for not using principal component analysis for analysing the vegetation data was justified in the review of the methods and is further born out by the fact that the first axis of the woody plant ordination is in excess of six half changes. This gradient is appreciably longer than can be successfully ordinated (without producing distorted axes) using principal component analysis (Gauch, Whittaker and Wentworth 1977).

Furthermore, ordination of the soils data using centered principal component analysis (data matrix standardized to unit variance) is considered more appropriate than their analysis using either reciprocal averaging or detrended correspondence analysis since soil attributes often show unidirectional if not strictly linear response curves (Williams, 1976).

A second possible criticism relates to the depth to which these data have been explored. To reduce the amount of variance involved, an obvious step in improving the understanding of relations between vegetation and environment would be to subset the data along the lines of the first two divisions of the two-way indicator species analysis

(i.e. Quarternary sand communities, communities on the Cretaceous deposits and communities of the volcanic rock formations) and then examine relations within these groups. These analyses have in fact been done, but are not presented here in any detail, since the level of insight achieved and the detail involved in the discussion of the results goes beyond the requirements for this part of the study.

3.5.2 Results

3.5.2.1 Soil ordination and classification

The first two axes of the soil ordination captured 64% of the variation in the soils data. The dissimilarities in the samples grouped towards the poles of each axis were reinforced by the geological substrate from which they were derived and by their position on the catenal gradient.

Several clear discontinuities are evident in the soil ordination, resulting in the easy delineation of four major groups of soils, viz. lithosols, arenosols, duplex soils and a heterogeneous group comprising base rich clays, sandy clay loams, sandy loams and lithic soils. Within these major groups there are no sharp discontinuities in the distribution of samples.

The soil classification presented in Appendix 2 describes 19 soil types, not all of which can be distinguished or separated on the aerial photography. For instance, the red sandy clay loam soils grade into the red clays down the catenal gradient without any clear surface indication of this change. A second example of this is found within the 'non-duplex brown calcimorphic soils' which consists of 28 samples. This is subdivided primarily on texture into 'yellow brown sandy loam to sandy clay loams', but while the end samples in this gradient can be easily distinguished, no clear discontinuity is apparent.

The predominance of gradients of change as opposed to sharp discontinuities between soil types is also common within the arenosols, alluvia, lithosol and lithic soil groupings. In general then, it is apparent that ordination and classification have complemented one another in explaining the structure in these data. The fact that the data could have been explored in greater depth is

irrelevant, since some soil types at the present level of delineation are not viable at the chosen scale of mapping.

3.5.2.2 Vegetation ordination and classification

The ordination of woody and herbaceous data proved satisfactory in that the first two gradients at least were both biologically and environmentally interpretable. The first axis of the woody plant ordination, representing a sand to clay gradient, showed a sharp discontinuity between sites of sandy soils and sites found on all other substrates. This discontinuity was also reflected in the two-way indicator species analysis of these data.

The second axis, reflecting a gradient from shallow lithosols on the crests of the Lebombo Mountains to sandy clay loams in the bottomlands, had a minor discontinuity between sites found on the shallow lithosols and sites on all other substrates. Again this was reflected in the classification. From this point onwards, the ordination was less useful in assisting the classification, but no less useful in interpretating environmental gradients within the three major groups, viz. samples on lithosols, sand and soils derived from the cretaceous sediments.

The vegetation classification presented in Fig. 21 defines 20 major types, some of which have been subdivided. Failings of the classification are that all types are not equally dissimilar, some are not viable from an environmental point of view (notably type 5) and some do not form viable mapping units. The classification's strength lies in its hierarchical structure and the flexibility it allows users in choosing the level to which sample allocation should proceed.

Within the three major groups mentioned above, few clear discontinuities are evident in species composition and complex disturbance and environmental gradients appear to govern variation in species composition and structure. For this reason, vegetation physiognomy becomes more prominent in the allocation of samples to groups at the lower levels of the hierarchy.

3.5.3 Vegetation stability and dynamics

Although classification is not aimed at developing an understanding of the dynamics of vegetation change, environmental interpretation of the classification assisted by ordination can give some insight into the direction of change and relative stability of the suggested communities. With the incorporation of the available historical information, a fairly good but broad interpretation of the vegetation dynamics may be obtained.

Observed changes in the vegetation of Mkuzi

Anecdotal information from previous occupants of the reserve and more recently rangers reports, indicate that there have been large fluctuations in vegetation biomass and in particular in the herbaceous layer. These fluctuations in herbaceous production are most likely caused by the large fluctuations in rainfall. However, the general impression gained from these comments is of a shift in the composition of the herbaceous sward, initially dominated by tall tufted perennial grass species with good cover to one which is now characterised in places by an extremely poor cover of annual grasses and forbs. This seems particularly true of the plant communities dominated by *Acacia tortilis* found on the calcareous yellow-brown sandy clay and sandy clay loam soils situated in the east of the reserve, and also the mixed *Acacia* spp. communities found on the red sandy clay loam and clay soils. The main exceptions to this trend are all the plant communities associated with the lithosols on the Lebombo foothills and found in the extreme west of the reserve. Here the grass cover appears to have remained in a state dominated by tall tufted perennial grasses with little or no comment as to whether changes have occurred.

The earliest (1937) and subsequent (1955, 1963, 1972 and 1975) aerial photographs of the area tend to corroborate the above assertions. Aerial photographic analyses, however, are far better suited to detecting changes in tree and shrub canopy cover and in this instance, several interesting observations have been made.

Firstly, in the period under review (1937-1975), extensive areas to the east of the reserve on calcareous yellow-brown sandy clay loam and sandy clay soils have shown a marked increase in woody canopy

cover. The most important species responsible for this are *Acacia tortilis* and to a lesser extent *Acacia nilotica*.

Secondly, and by contrast, the communities found on the lithosols of the Lebombo foothills have with few exceptions remained wooded grasslands and little or no increase in woody cover can be detected. The exceptional areas in this landscape are old lands which were cultivated by previous occupants of the reserve. The most important woody species that have shown an increase in density in this instance are *A. nilotica* on north facing (drier) slopes and *A. karroo* on the south facing slopes. In both instances the soils show varying degrees of sheet erosion and the deflated soil surface is now characterized by a grit and stone mantle. The return of a grass cover to these areas appears to have been determined mainly by the intensity of grazing subsequent to the abandonment of the cultivated land.

Thirdly, the forest, closed woodlands and woodlands found on sandy soils have shown few detectable changes in woody plant density. Again exceptions to this are areas of major disturbance, namely areas of previously cultivated lands and areas around artificially introduced waterpoints. Perturbations such as these have resulted in the development of *Xeromphis obovata* thicket and scrub on the red sands and loamy sands. Distinct boundaries of communities such as the *Cleistanthus/Croton* spp. Sand Forest, have remained remarkedly stable over the period 1937 to 1975.

Fourthly, and primarily in the east of the reserve, the bushland, thicket and scrub communities found associated with the low lying melanic clay and heavy clay pan soils have shown marked changes. These are:

i) periferal extension primarily by *Euclea divinorum* into what were alternating wet (rainy season) and dry (dry season) grasslands and wooded grasslands,

ii) an increase in broad leaf evergreen woody plants (mainly *Euclea* spp.) in the *Acacia luederitzii* thickets and scrub,

iii) a complete change in some wooded grassland communities previously dominated by *Acacia nigrescens, A. nilotica* and *A. tortilis*, to an open bushland. The latter are now characterized by a tall open upper canopy of senescing *Acacia* trees (normally *A. nigrescens, A. tortilis* or *A. nilotica*) and

a much denser lower subcanopy of *Euclea* spp.. This 'succession' from wooded grassland to scrub, thicket and bushland is more fully described by Smith and Goodman (1987).

Possible causes of vegetation change

Herbivory

Prior to the 1830's Mkuzi was part of a much larger wildlife ecosystem. It is semi-arid, with largely base-rich soils, a poor dry season surface water distribution and is situated adjacent to the high rainfall, leached sandy soil areas typically found to the east of the reserve on the remainder of the coastal plain. Mkuzi would thus have formed the wet season range for the large migratory herds of wildebeest and zebra which occupied the area at the time. In addition, large herds of elephant and eland were reported from the area.

The period between 1830 and 1950 saw the mass reduction of game animals by hunters, the rinderpest epidemic in the late eighteen hundreds, and farmers in an attempt to eradicate *Trypanosomiasis* (nagana). By 1950 elephant were only occasional visitors to the reserve, the large migratory herds of zebra and wildebeest were much reduced and sedentary while eland were totally extinct from the region.

Between 1950 (when management of the reserve was assumed by the Natal Parks Board) and 1960 populations of smaller herbivores increased rapidly resulting in the initiation of game control operations in 1963. During this period permanent water was introduced to the reserve and with the increase in human populations around the reserve, the large herbivores became more and more restricted to the reserve.

The period 1830 to 1960 thus saw large changes in the nature of herbivory occurring in the reserve. During the early 1800's the system was probably dominated by migratory herds of selective grazers (wildebeest and zebra), a large but variable biomass of large mixed feeders (elephant and eland) and a much smaller biomass of obligate browsers (black rhino and kudu) and small mixed feeders (impala and nyala). By 1960 the system had become dominated by sedentary

intermediate sized mixed feeders (impala and nyala) and selective grazers (wildebeest and warthog).

Other factors

Other factors thought to have influenced the vegetation dynamics are changes in fire frequency, the drought in 1935 and the anti-nagana D.D.T. spraying campaigns undertaken between 1945 and 1950.

Historically, fire in this area was used extensively as a tool for managing vegetation. The primary purposes of burning were; a) to assist in hunting by attracting game to new vegetation growth, which takes place after the burn, and to clear the undergrowth so as to ease the chase by dogs, and b), on a more local scale to assist in the clearing of fields for cultivation. Occasionally, fires were accidentally started by careless honey collectors who were using smoke to ease access to the honey. The frequency of burning was governed by fuel load and fires were started from a point source from the onset of the dry season. The spacial extent of individual fires was determined by the prevailing weather conditions, and distribution of the fuel load. It is thought that unless rain curtailed the further use of fire during the dry season, most of the area (in particular the Lebombo foothills) was burnt on an annual basis.

With the assumption of management by the Natal Parks Board in 1950, the frequency with which fire was applied to the reserve was reduced considerably. Infrequent accidental fires did occur in the reserve between 1950 and 1965, which is when the first control fire was implemented by management. Since 1965, the area with the most frequent burning regime has experienced fire once every 2 to 3 years. This reduction in fire frequency would have allowed an increase in woody plants at the expense of grasses.

The drought which occurred in the 1935/36 season was until recently the worst on record and it was at this time that eland were thought to become extinct from the entire region. This drought is thought to have resulted in the almost complete denudation of the herbaceous cover over large areas, and thus as a result of reduced competition from the herbaceous layer and the temporary absence of fire, the germination and recruitment of pioneer *Acacia* spp. such as *A. tortilis*, *A. nilotica* and *A. grandicornuta* took place. In the

years to follow, the reduced number of browsing animals, and in particular elephant, would have allowed many of the woody plants recruited during this period, to grow to maturity. Herbivory, particularly by a large destructive browser such as elephant has had a large impact on the physiognomy of African vegetation (see Buechner and Dawkins 1961; Lamprey, *et al.* 1967; Harrington and Ross 1974; Pellew 1983) and in particular *Acacia tortilis*, which is highly favoured by elephant. For these reasons it is suggested that the 1935/36 drought and the absence of elephant were probably the major factors contributing to the increase in woody plants and in particular *Acacia tortilis* in recent times.

Between 1945 and 1950 anti-nagana D.D.T. spraying was undertaken in the reserve. By all accounts, *Glossina* spp. were not the only insects to fall prey to the poison treatment and undoubtedly the parasitic seed beetles (*Bruchidius* spp.) were also affected. Species of the latter genus are known to infest a high proportion of *Acacia tortillis* seeds in Tanzania (Lamprey, *et al.* 1974) and it is quite likely that reduced seed predation resulted in an increased bank of viable seed, and later allowed for a greater recruitment of *Acacia* spp. into the existing population.

Vegetation stability and successional tendencies in the major land units

On zonal soils (generally described as brown calcimorphic soils cf. Young, 1976), the climate of Mkuzi is thought to give rise to woodland, bushland and dry forest as the zonal vegetation type (Walter, 1971; Holdridge, *et al.*, 1971). Wooded grasslands and grasslands under this climatic regime are thought to be induced and maintained by human influence, fire and herbivory. Exceptional edaphic factors such as seasonal water logging of the profile or shallow lithosols are thought to give rise to the generally azonal wooded grasslands and grasslands. Thus we would predict an increase in woody vegetation if any or all controlling influences were removed. As described in the previous section, it is apparent that for the

zonal soil type this has to a large degree proved true, and consequently, I will now comment on the stability and successional tendencies of the vegetation in the major land units.

The major plant associations on sands (see Fig. 21) appear to be fairly strongly associated with edaphic factors, and are stable and resistant to change. The erection of a large herbivore exclosure on red loamy sands has shown no major changes other than the accumulation of a large amount of herbaceous biomass and an increase in the proportion of erect, tufted and palatable grasses.

The Lebombo foothills land unit consisting mainly of lithosols (Fig. 21), has four major vegetation subdivisions and all appear to have been subjected to fairly frequent fires in the past. The origin and maintenance of the physiognomy of the communities comprising this land unit can be attributed to the combined effects of a number of interacting factors, viz.:

i) Rocky substrate, consisting of a shallow soil covering massive flows of larval rock. This provides limited rooting opportunities for trees, yet the shallow soil is able to sustain a good cover of tall, tufted perennial grasses.

ii) Trees which become established have shallow root systems and are suseptible to being blown down in the event of strong winds.

iii) The rockiness of the terrain and great distance to permanent water, has discouraged the development of a high biomass of sedentary grazers, the resultant grazing pressure is relatively low and therefore the grass biomass is high.

iv) Maintenance of a high grass biomass facilitates the opportunity for frequent fires, both natural and man induced. Frequent fires further discourage woody vegetation which encourages more grass.

Under these circumstances, this land unit appears quite resilient to minor perturbations such as drought and changes in burning frequency, and in the long term would appear to show a high degree of stability. More severe perturbations such as clearing and cultivation have all resulted in marked changes. These changes have been almost exclusively restricted to the moister south facing slopes and bottom lands, where soils are slightly deeper. In all instances, the

perturbation has reduced the herbaceous cover, increased run off and surface soil erosion, reduced the effect of fire and resulted in an increased density of woody plants, primarily *Acacia karroo*. West and north facing slopes appear extremely stable even to prolonged heavy grazing.

The mixed *Acacia* spp. wooded grasslands (Fig. 21), found primarily on the red clay loam and sandy clay loam soils derived *in situ* from Lower Cretaceous deposits, appear relatively stable under the present regime of climate and utilization. Few marked changes have occurred since 1937. Those changes which are thought to have taken place namely;

i) a general reduction in the herbaceous biomass and a relative increase in forbs and annual and/or highly unpalatable grasses such as *Bothriochloa insculpta*,

ii) an increase in shallow rooted shrubs such as *Dichrostachys cinerea* and *Maytenus senegalensis*.

The cause of these changes is thought to be due primarily to an increase in grazing pressure brought about by the redistribution of surface drinking water. Here and in other communities in the reserve there appears to be an even age distribution of the dominant woody plants (*Acacia nigrescens*, *A. tortilis* and *A. gerrardii*) and it is interesting to speculate about the mechanisms underlying this land type's apparent stability. A current hypothesis suggests that the present mixture of woody plants and grasses are maintained in a stable equilibrium by means of a two-layed soil water condition (Walker and Noy-Meir, 1982; Walker, *et al.*, 1981) or by competition between perennial grasses and germinating woody plants and seedlings for soil moisture (Walter, 1971).

The presence of a two-layed soil water condition in this situation is doubtful due to the slope of the terrain and the relatively high clay content of the soils (30 - 40%). In addition soils are not deep (<1 m) over most of this area and are underlain by a fairly porous saprolite. Lack of establishment and survival of woody seedlings through competition with perennial grasses also does not meet with much support in this instance, simply because there are a large number of well established woody seedlings throughout the herbaceous layer. Instead, an alternate hypothesis suggesting that the combined effect

of intraspecific competition and heavy browsing pressure is the major determinant of this areas physiognomy seems more acceptable. The evidence for intraspecific competition is detailed in Smith and Goodman (1986) and will not be presented here. That browsing pressure by herbivores is having a marked effect on plant stature is well illustrated by a herbivore exclusion experiment in this land unit where a marked increase in the growth rate of woody plants inside the exclusion plot compared to the control was noted.

Of all the land units in Mkuzi the *Acacia tortilis* bushlands, woodlands and wooded grasslands (Fig. 21) occurring on yellow-brown calcareous sandy clay loam and clay loam soils, have shown the most change over the past thirty five years. The probable reasons for these changes were given in the previous section. In addition, it does not appear as though the present state of this land unit is stable. In general these *Acacia* communities are characterised by low *Acacia* spp. recruitment rates in the under canopy environment. Again this is not thought to be a result of a two-layered soil water condition or as a result of competition with perennial grasses simply because grasses in general, form an extremely minor component of the ground cover. Instead intraspecific competition for resources is much more likely to give rise to this situation (Smith and Goodman, 1986). For the present, the sub-canopy environment is characterized by a marked increase in evergreen and semi-deciduous shrubs such as *Euclea divinorum, Azima tetracantha* and *Ehretia rigida*. The likelihood of the present *Acacia* spp. canopy being replaced by a variety of broad leaf species is high and has been witnessed elsewhere in the reserve on some of the more clayey soils. Since all three species are considered to be fire sensitive from a management view point, reversal of this 'succession' might be brought about through the judicious use of fire. However, since flammable grass forms an extremely small proportion of the herbaceous biomass at the end of the dry season this option is not feasible. Instead the halting and possible reversal of this trend would be more probable through herbivory, especially since *Acacia tortilis* and *Azima tetracantha* are considered favoured foods of elephant.

The bushlands and thickets (Fig. 21), found mainly on dark calcareous clay soils, appear to be physiognomically quite stable.

The herbaceous layer consists primarily of unpalatable perennial or palatable stoloniferous grasses. The woody plants are normally dense shrubs, a large proportion of which are either unpalatable (*Euclea* spp., *Cassine* spp., *Sideroxylon inerme*) and/or unpalatable and armed with thorns (*Acacia luederitzii* and *A. grandicornuta*). With an increased infiltration brought about by the accumulation of leaf litter on the soil surface, improved soil moisture conditions and the increase in shading, it seems that the apparent increase in the broad leaf evergreen component of the woody vegetation, at the expense of the microphillous component will continue (Smith and Goodman, 1987).

CHAPTER 4. LARGE HERBIVORE COMMUNITY STRUCTURE AND DYNAMICS

4.1 INTRODUCTION

The purpose of this chapter is to describe the composition, distribution, abundance and general dynamics of the major large herbivore species in Mkuzi. The spatial distribution of herbivore impact is also described, followed by a general historical backround to large herbivore exploitation and an analysis of the recent dynamics of the most prominent species.

4.2 METHODS

4.2.1 Population estimation

The primary means of large herbivore census was based on line transect sampling as reviewed by Burnham, Anderson and Laake (1980). A system of initially 8 and later 13 ground transects were located so as to sample as wide a spectrum of land types and vegetation as was practically possible in the time available for censusing (Fig. 22). During each annual census which was undertaken towards the end of the dry season, each transect was replicated in time at least eight times. Field data for each herbivore sighting consists of species, location along the length of the transect, group size, distance to the geometric center of the group and the angle of this latter position relative to the direction of travel.

Density estimates were derived using the following general relationship:

$$D = n.f(o)/2L$$

Where D - group density estimate

n - number of groups seen

$f(o)$ - probability density function at zero distance from the line

L - total length of transect walked.

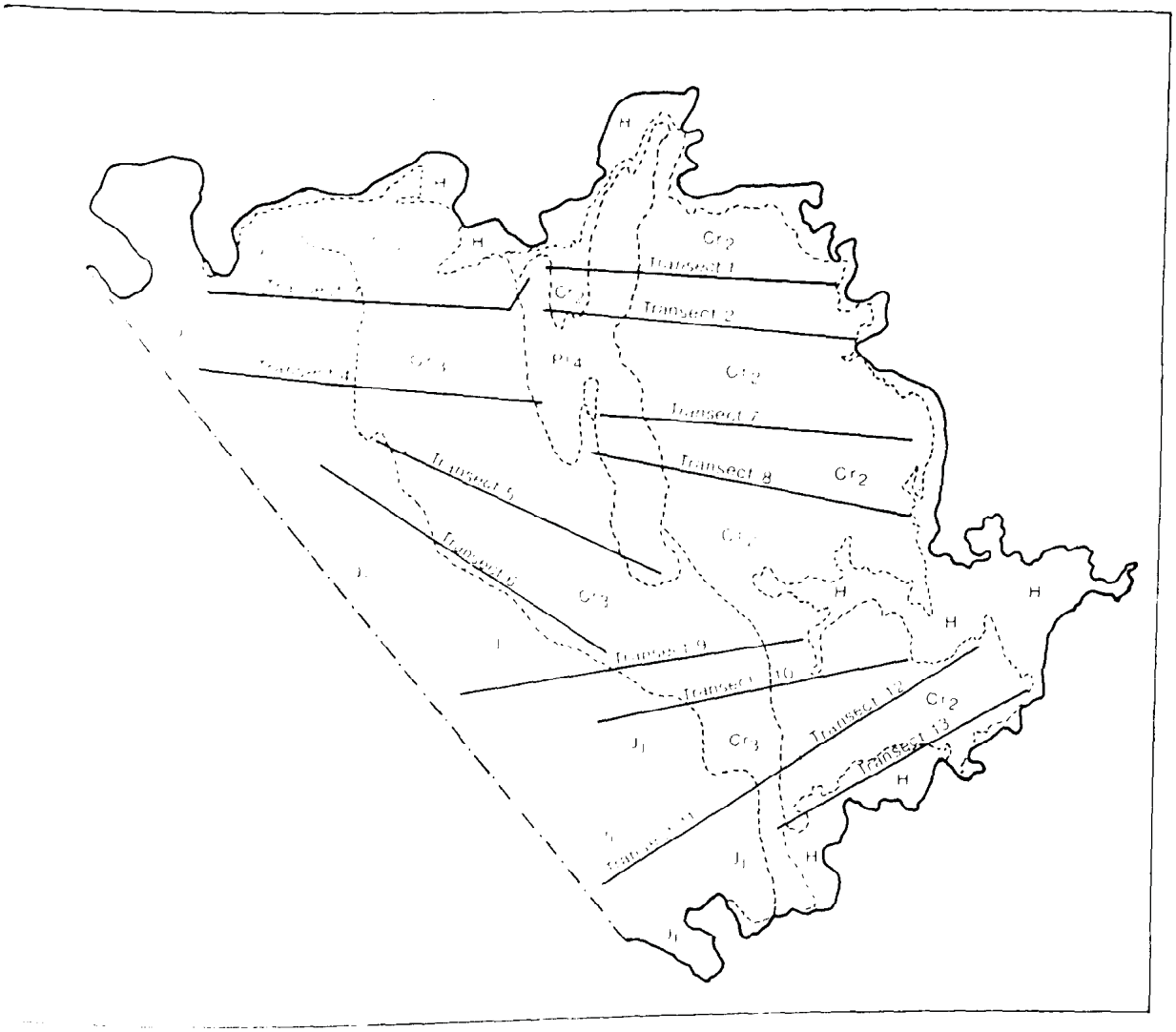


Fig 22 Location of the thirteen ground census transect in relation to the five land types found in Mkuzi. Land type abbreviations are J_J - Lebombo hill area, Cr_3- Lower Cretaceous undulating terrain, Cr_2 - Upper Cretaceous plain, Pl_4 - Pleistocene dune cordon and H - Quarternary alluvia and floodplain.

The estimation of f(o) was based on the Fourier series expansion of the probability density function. The method is covered in detail by Burnham, *et al.* (1980).

Species whose populations were either nocturnal (bushpig), aquatic (hippo) or too small to estimate using a sampling technique, were treated differently. For the last of these, known groups were tallied for each species, and hippo were counted from fixed wing-aircraft. A subjective estimate of population size of each nocturnal species was made.

Prior to 1980 large herbivores were censused using a variety of other techniques including helicopter aerial census, road strip census and a change in sex ratio method (Stewart and Stewart, 1966). In conjunction with the hunting data from the last Nagana campaign, all census results are used to examine the recent population dynamics of herbivores, as well as to examine changes in community structure.

4.2.2 Stocking density estimation

The biomass density was calculated for each herbivore in each land type by multiplying the density of each herbivore by its mean mass (Table 5). In addition the relative energy consumption of each species was determined and expressed in animal units (AU) where the AU equivalent for each species was calculated as: $455^{0,75}$/mean $mass^{0,75}$ (Table 5).

4.2.3 Graze to browse ratio

The relative amount of energy derived from non-graminaceous food sources (i.e. browse) was estimated by multiplying the relative energy consumption of each species by the mean proportion of browse making up its diet. These were then summed up for all species and expressed as a proportion of the total relative energy consumption per unit area. The proportion of browse in a herbivore diet is in reality not a constant but varies seasonally and between areas depending on the availability of preferred food. Gross estimates of the proportion of browse making up the relevant species diet are bushbuck 0,9, grey duiker 1,0, red duiker 1,0, eland 0,75, giraffe 1,0, impala 0,2, klipspringer 0,9, kudu 0,9, nyala 0,6, black rhino 1,0, steenbok 0,8

and suni 1,0. No correction has been made for the difference in energy content of graminaceous vs non-graminaceous food sources. This is therefore likely to over emphasize graze as a source of energy.

Table 5. Mean mass (kg) and Animal Unit equivalents for large herbivores encountered in Mkuzi.

Species	Abbrev.	Mass	AU Equivalent	Authority
Bushbuck	Bb	30	7,68	1
Bushpig	Bp	54	4,95	1
Duiker/Grey	Dg	17	11,77	Western (1979)
Duiker/red	Dr	14	13,61	Smithers (1983)
Eland	El	340	1,24	1
Giraffe	Gi	750	0,69	1
Hippo	Hi	1000	0,55	1
Impala	Im	40	6,19	1
Klipspringer	Kl	12	15,28	Smithers (1983)
Kudu	Ku	136	2,47	1
Nyala	Ny	60	4,57	Anderson (1978)
Reedbuck/Common	Rc	50	5,24	Venter (1979)
Reedbuck/Mountain	Rm	28	8,09	2
Rhino/Black	Rb	816	0,65	1
Rhino/White	Rw	1500	0,41	1
Steenbok	St	11	16,31	Smithers (1983)
Suni	Su	5	29,46	Smithers (1983)
Warthog	Wh	45	5,67	1
Waterbuck	Wa	160	2,19	1
Wildebeest	Wi	165	2,14	Attwell (1977)
Zebra	Ze	200	1,85	1

Authority 1 - Coe, Cumming and Phillipson (1976).
2 - Mentis and Duke (1976).

4.3 RESULTS

4.3.1 Density estimates

When considering the reserve as a whole, impala (20,6 km^{-2}) and nyala (11,1 km^{-2}) were by far the most numerous large herbivores (Table 6 and Fig. 23), followed by warthog, zebra, grey duiker, kudu, wildebeest, bushpig and red duiker which occurred at densities that were less than 3 but more than 1 km^{-2}. Densities of the remaining species were all less than 1 km^{-2}.

Impala were the most numerous large herbivore in the more open woodlands of the Lebombo hill area and the two Cretaceous land types, but in the more dense woodlands found on the Pleistocene dune cordon and the Quarternary alluvia, nyala dominated (Table 6). Zebra were the second most abundant large herbivore in the taller grass areas associated with the Lebombo hill land type, but achieved peak densities (2,48 km^{-2}) on the Lower Cretaceous land type. Warthog rated the third most abundant species on the Lower Cretaceous land type, which is where they achieved their peak density (3,42 km^{-2}). Kudu were the third most abundant large herbivore on the Upper Cretaceous plain, but achieved peak densities (5,68 km^{-2}) in the denser woodlands found on the Pleistocene dune. Grey duiker also achieved peak densities (7,57 km^{-2}) on the Pleistocene dunes where they ranked the third most abundant large herbivore (Table 6).

4.3.2 Biomass density and relative energy consumption

The mean herbivore biomass for the reserve as estimated in August 1984 was 3447 kg km^{-2}. This ranged from a maximum of 5178 kg km^{-2} on the recent dunes to a minimum of 2311 kg km^{-2} on alluvium (Table 7). Mean relative energy consumption was estimated as 11,8 AU km^{-2}, with a maximum of 17,1 AU km^{-2} and a minimum of 8,5 AU km^{-2} on the dune and alluvial land types respectively (Table 8). Whether herbivore importance was expressed as biomass or in AU, the rank order achieved by each land type in terms of its importance to large herbivores was the same (Tables 7 and 8). This also held true with few exceptions in a ranking of herbivores (Fig. 24 and 25). For this reason only the results of relative energy consumption are discussed.