applied to the sample scores at each iteration, but once convergence is achieved the final sample scores are derived by weighted averages of the species scores without detrending. The third axis is calculated by detrending sample scores with respect to the second as well as the first axis and so on for higher axes. This procedure results in an eigenvector ordination of variates with no arch effect. In this instance however, the sample scores are as in reciprocal averaging the weighted averages of the species scores. The second problem, compression of species and stands at the ends of the first axis is rectified by expanding or contracting small segments along the species ordination axis so that species turnover occurs at a uniform rate along the species ordination axis. A result of this rescaling is that the length of ordination axis becomes a real measure of the rate of species turnover (beta-diversity) along the axis. The unit of measurement is the average standard deviation of species turnover (SD) where a full turnover of species occurs in about four SD and a 50 per cent change in sample composition occurs in about one SD. The advantage of this is that it allows comparison of ordination results from different data sets (Gauch, 1982).

To summarize, detrended correspondence analysis ordinates samples and species simultaneously, objectively, efficiently and effectively and appears to be the most successful technique in when applied to species by sample matrices with high beta - diversity (Gauch, 1982).

Two-way indicator species analysis

Two-way indicator species analysis (Hill, 1979b; Gauch, 1982) is a polythetic divisive classification technique akin to ordination space partitioning, but differs from the latter by partitioning automatically and in an objective way. The basis of the technique is firstly an ordination of the data using reciprocal averaging. Samples are then polarized by emphasizing the species which characterize the ordination axis ends. Samples are then divided into two clusters by partitioning the ordination axis near its middle. The division is then refined by reclassifying the samples using species that are strongly associated with the poles of the ordination. This process is repeated on the two sample subsets to give four clusters and is repeated until each cluster contains no more than a chosen minimum number of samples. Simultaneously a species classification is produced and the sample and species classifications are used to produce an arranged matrix similar to that produced by a Braun-Blanquet table arrangement. One of the advantages of this technique over other polythetic divisive classifications is the emphasis it places on indicator species. This allows for easy group identification of new samples which may be further aided by a dendragram of the sample hierarchy. Gauch (1982), considers two-way indicator species analysis effective, robust and superior to other forms of hierarchical classification.

Canonical variate analysis

Canonical variate analysis (Williams, 1976; Jeffers, 1978), also called multiple discriminant analysis (Pielou, 1977) is a statistical technique used primarily to find a linear combination of variates that will allow for the best discrimination between groups supplied from an a priori classification. Canonical variate analysis emphasizes the between group variability at the expense of within group variability, the object being to derive a set of discriminant functions or canonical variates which minimise the confusion between one group and another.

Once the discriminant functions have been calculated, they can be used to study the spatial relationships of groups in reduced dimensions, such as is the case for variates and samples in principal component analysis. In instances where group membership is uncertain or new samples need to be allocated to a group, canonical variate analysis may be used as a classification technique.

The procedure for classification involves the use of separate linear combinations of the discriminating variables for each group. From these a probability membership for each respective group is calculated. Samples are then assigned to the group with the highest probability. This assignment or classification can then be compared to the assignment of samples in the a priori classification and the group membership adjusted accordingly.

The theory of canonical variate analysis requires that the initial data (discriminating variables) are substantially multivariate normal and that each group has variance-covariance matricies of similar magnitude. Although these conditions can rarely be fulfilled, it seems that the technique is very robust to these assumptions (Nie, Hull, Jenkins, Steinbrenner and Brent, 1975) and as long as the technique is used for data reduction and exploration (as apposed to hypothesis testing) they need not be strongly adhered to.

Orloci's sums of squares methods

Orloci's sums of squares method (Orloci, 1967; Goldstein and Grigal, 1972; Pielou, 1977) or minimum variance clustering (Gauch, 1982) is a hierarchical polythetic agglomerative technique using the within-group sum of squares as the agglomeration criterion. The method operates on metric (standardised or unstandardised) distance and the within-group dispersion of a group is defined as the sum of squared distances between every point and the groups centroid. At any stage two groups (or individual samples) are combined providing that the increase in within - group dispersion resulting from the union is less than it would be had either of the groups been joined with some other group (or individual sample). Agglomeration is carried out in successive cycles, the process resulting in a dichotomously branching hierarchy.

The use of the centroid as each group's location in species space is in contrast to the "naive methods" (Pielou, 1977 referring to other single and complete linkage clustering techniques) and to a large extent avoids the major problems of these methods which are, "chaining" (single linkage clustering) and the formation of unnatural classes comprising groupings of samples dissimilar to all other samples or groups (complete linkage clustering).

Minimum variance clustering is similar to average - linkage clustering the latter being recommended by Sneath and Sokal (1973) as best for generalized hierarchical classification. The advantage of minimum variance clustering over average - linkage clustering is that using squared distance instead of average distance makes clusters in the former tighter than in the latter (Gauch, 1982).

3.3.3.2 Data transformation and editing

Soils

Because of the difficulty with analysing mixed data sets (consisting of qualitative as well as quantitative data), only those variates measured quantitatively were used in the multivariate analysis, this included 17 variates from 118 sample sites. Two variates, total exchangeable bases and total exchangeable bases per 100 g clay, were excluded from the analysis since they were recombinations of other variates, namely sum of cations and sum of cations divided by clay percentage respectively. Variates were measured in a variety of different units, and thus had different ranges and variances, it was therefore necessary to standardise the data prior to analysis (Webster, 1977; Williams, 1976). This was done by using a correlation matrix as the starting point for principal component analysis and centering the data to unit variance prior to classification by Orloci's sums of squares method.

Vegetation

The difficulties in making comparable estimates of cover abundance for herbaceous and woody vegetation, necessitated their separate analysis. In addition, the type and magnitude of environmental factors influencing these two strata vary to a large extent and in order to elucidate these, their separate analysis was necessary.

Herbaceous data consisted of a matrix of cover abundance values for 370 species in 118 sample stands. Data editing excluded species which had three or less occurrences in the data matrix, were unreliably identified and which were ephemeral in their growth habit. This left a total of 96 herbaceous species.

Woody vegetation was treated differently. Initially trees were analysed separately and then were combined with shrubs into a single data set and analysed together. Prior to all analyses sample stands without species and species occurring three or less times in the data matrix were removed. This resulted in a 64 species by 116 stands and a 162 species by 118 stands matrix for tree and combined tree and shrub data sets respectively.

3.4 RESULTS

3.4.1 Soils and land types

3.4.1.1 Soil ordination and classification

Summary statistics for soil variates are presented (Appendix 1). Using the normal significance test (a test of doubtful validity in this instance, see Jeffers, 1978; Williams, 1976) there appeared to be a high degree (74%) of correlation between variates (Appendix 1, Table A 1.2). The only variate to show a low degree of correlation with others and thus appearing to be independent of these was phosphorus.

The results of the principal component analysis by the between variate (R) correlation matrix may be evaluated on examination of the latent roots (eigenvalue) and latent vector loadings for each variate on each principal component (Table 1). The results suggest that a limited number of dimensions are sufficient to account for the major variability found in the physical and chemical properties since the first four principal components accounted for 78% of the variance in the data set (Table 1).

The coefficients of the linear functions defining the components (or the latent vector loadings) may be used to infer some real meaning to the components, the size and the sign of each coefficient being an indication of the proportion of the variance each variate accounts for along that component (Table 1). The first component which accounts for 44% of the variance is essentially a contrast between high organic matter content, high proportion of clay and silt, and high magnesium and potassium contents at one end of the axis and high sand at the other end (Table 1 and Fig. 8). It represents a complex soil gradient with base rich, poorly drained clay soils at one end and base poor, well drained sandy soils at the other.

The second component, accounting for 20% of the variance appears largely related to soil depth, with shallow, gritty, rocky soils (expressed by high rock cover, high proportion of stones in the B-horizon and high proportion of grit) at one end of the axis and deep soils with an even consistency at the other (Table 1 and Fig. 8).

Table 1. Latent roots (eigenvalue) and latent vectors resulting from a principal components analysis of the between soil variate correlation matrix. P.C. = principal component.

Variate	Abbreviation	PC I	PC II	PC III	PC IV
Rock cover %	RC	-0,14	0,42	-0,07	-0,05
Grit %	GR	-0,17	0,40	0,09	-0,18
Clay A %	ClA	-0,31	-0,20	0,26	0,02
Silt A %	SiA	-0,30	0,02	-0,03	0,16
Sand A %	SaA	0,33	0.14	-0,18	-0,07
ph	pH	-0,19	-0,12	-0,61	-0,19
Organic matter %	OM	-0,32	0,11	0,07	0,08
Phophorus	P	-0,05	0,06	-0,42	0,77
Calcium (me%)	Ca	-0,27	-0,12	-0,24	-0,17
Magnesium (me%)	Mg	-0,31	-0,20	-0,05	-0,04
Potassium (me%)	K	-0,30	-0,04	0,24	0,17
Sodium (me%)	Na	-0,17	-0,20	-0,24	-0,47
Aluminium (me%)	Al	-0,12	-0,004	0,30	-0,04
Profile depth (cm)	Depth	0,15	-0,46	0,004	0,09
Clay B %	ClB	-0,25	-0,28	0,26	0,07
Silt B %	SiB	-0,29	0,06	-0,03	0,07
Stones B %	StB	-0,19	0,43	0,03	-0,08
Latent root	-	7,25	3,41	1,35	1,02
% variance	-	44,22	20,07	7,96	6,02
Cumulative %	-	44,22	64,29	72,25	78,27

The third component which accounts for 8% of the variance is largely a gradient of acidity with a high negative loading for pH and a strong positive loading for aluminium or exchangeable acidity (Table 1 and Fig. 8). The fourth component (6% of the variance) has a high positive loading for phosphorus and a strong negative loading for

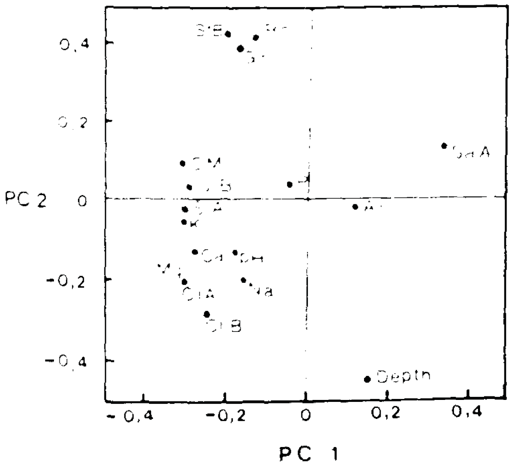

Fig. 8a Principal component analysis of soil variates. Variates plotted in the space defined by the first two principal components. See Table 1 for abbreviations

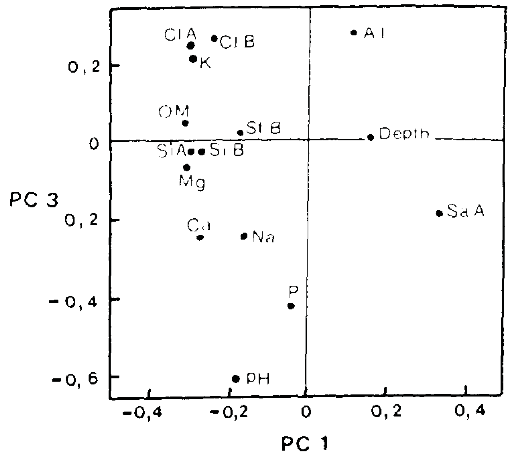

Fig. 8b Principal component analysis of soil variates. Variates plotted in the space defined by the first and third principal components. See Table 1 for abbreviations.

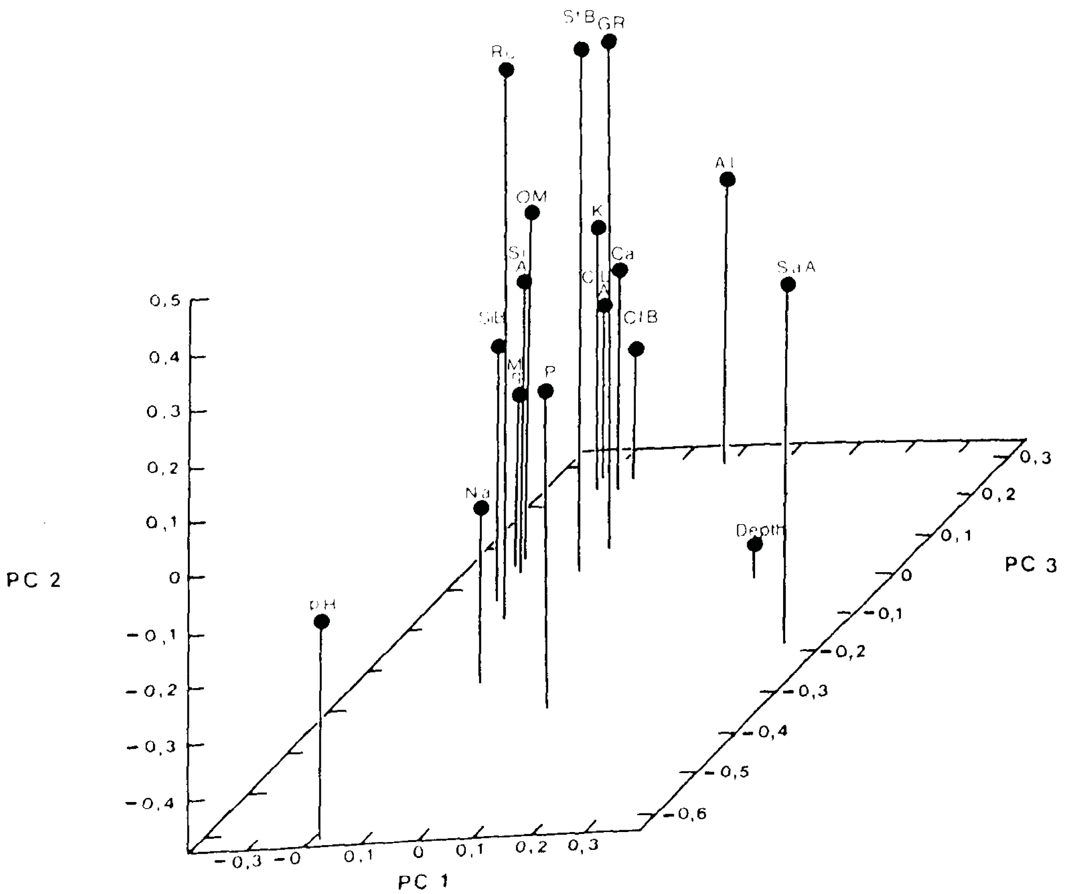

Fig. 8c Principal component analysis of soil variates. Variates are plotted in the three dimensional space defined by the first three principal components. See Table1 for abbreviations.

sodium, but no pedological meaning can be given to this gradient at present. Similarly the fifth and higher axes are uninterpretable.

To further assist the comprehension of these data each variate in the data matrix was standardized to unit variance prior to clustering using Orloci's sums of squares method (Orloci, 1967). At a classification efficiency of about 80% (ie. the within group mean squares expressed as a percentage of the sample mean square) two major groups are clearly evident (Fig. 9). The first consists of soils with a sandy A-Horizon (on average <5% clay) with low base status (T.E.B. on average <6 me%) and low organic matter content (organic matter <1%. The remaining samples form a diverse group, all characterised by having a higher clay content (>15%), higher nutrient status (T.E.B. on average >9 me%) and higher organic matter content (>1%) (Fig. 9). The group of sandy soils is well aggregated at the positive end of the first soil principal component axis, but is not disjointed from the rest of the samples indicating that there is a gradual transition from sands to loams and clays (Fig. 10a and 10b).

At a within group mean square of 55%, the group of 'diverse clay soils' is subdivided (Fig. 9), the main distinction being the amount of rock appearing on the surface or in the profile, the grit content in the A-horizon and soil depth. The result of this agglomeration is a group of shallow rocky or gritty base rich clay soils (means of rock cover >15%, grit >30%, depth <43 cm and the amount of stone in the B-horizon in excess of 85%) and a remaining group of deeper non-rocky, non-gritty base rich soils (means of rock cover <4%, grit <12%, depth >90 cm and the amount of stone in the B-horizon <30%). The group of shallow rocky base rich clay soils (base rich lithosols) is clearly separated on the second component in the soil principal components analysis (Figs. 10a and 10b).

At a classification deficiency of about 45%, the deeper non-rocky soils are subdivided into a group of sandy clay loam to clay soils with grit (means of clay content >31%, mean silt content >13% and mean grit >3% and sandy clay loam soils without grit (means of clay <28%, silt <15% and grit mean <1,5%). The latter group has an average base status lower than the former (Fig. 9). This separation appears fairly sodium, but no pedological meaning can be given to this gradient at present. Similarly the fifth and higher axes are uninterpretable.

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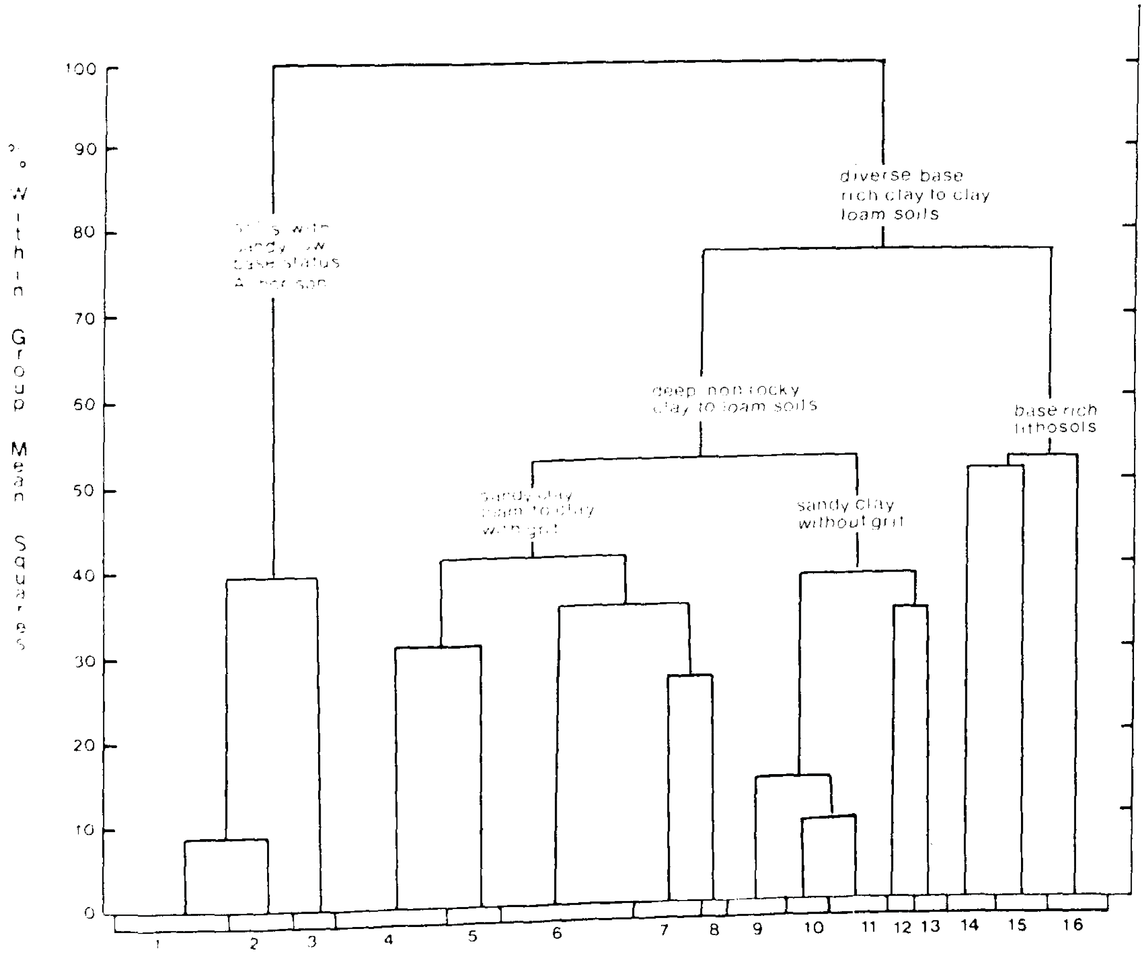

Fig 9 Hierarchical agglomerative clustering of soil samples. Data were standardized to unit variance and clustered according to the minimum dispersion criterion of Orloci (1967).

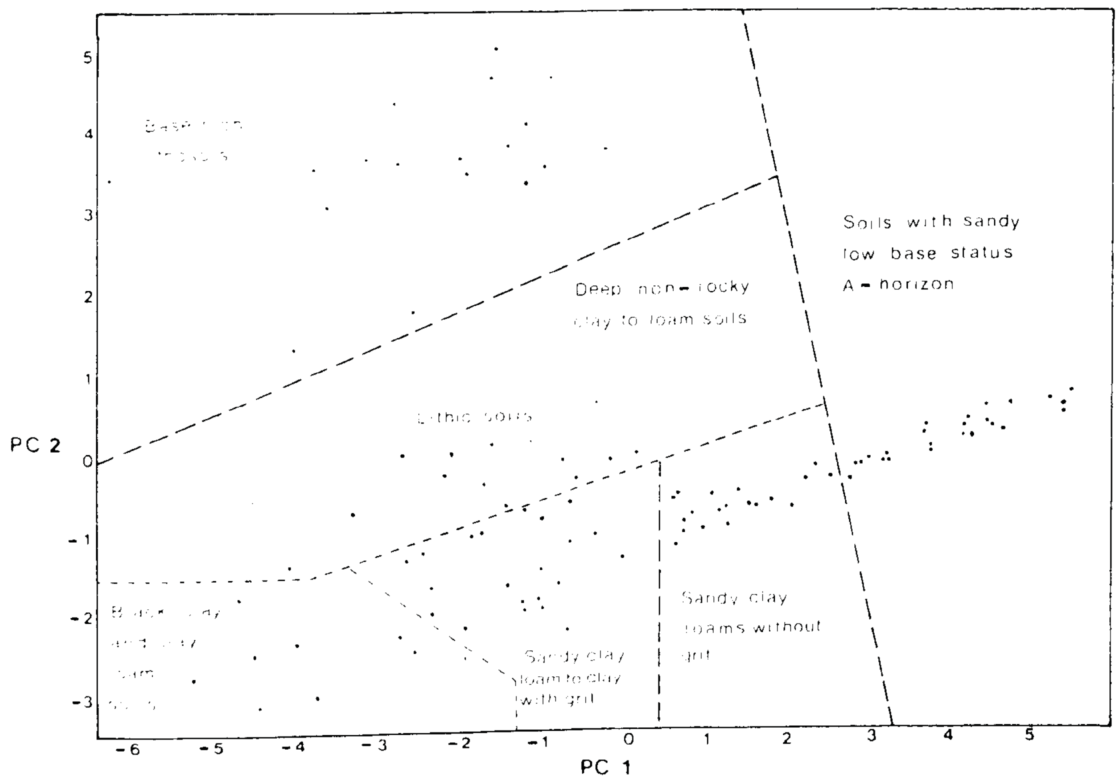

Fig. 10a Soil sample sites projected on to the plane of the first two principal components, from the soil principal component analysis.

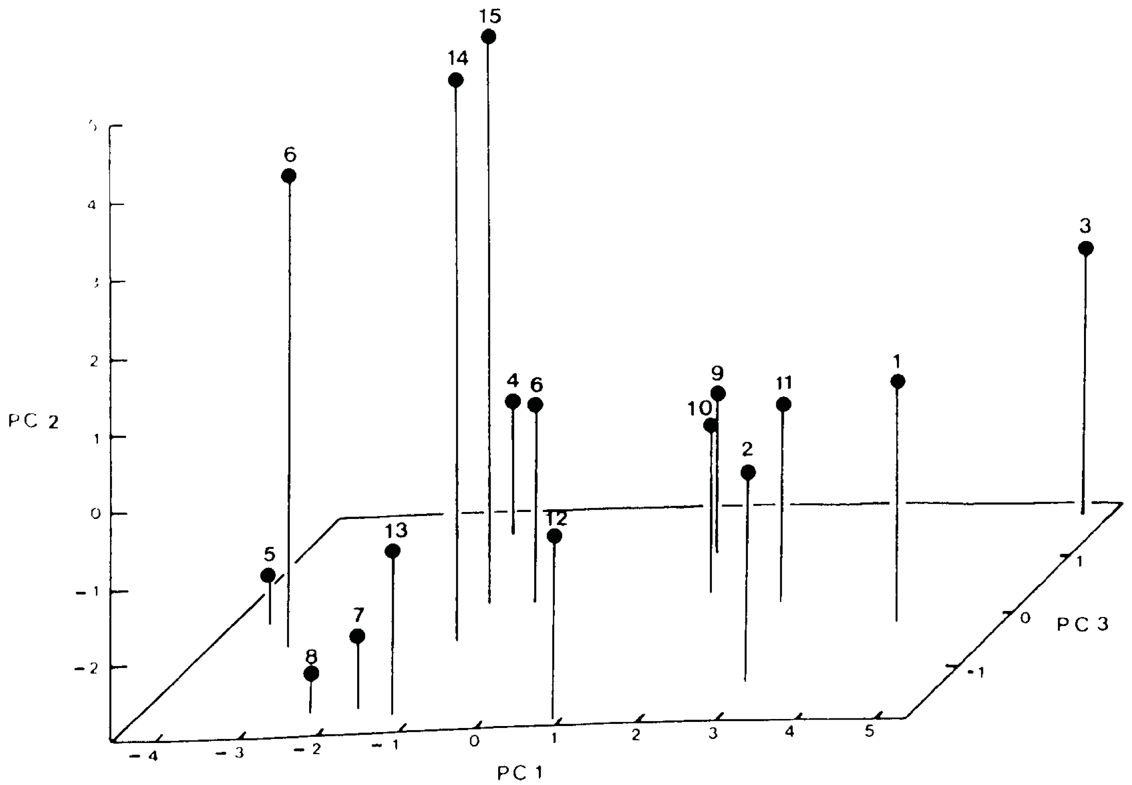

Fig. 10b Three dimensional plot of axis means for each soil group in the space derived from the first three principal components. The groups and their numbers were derived from the hierarchical cluster analysis (Fig. 9).

clearly on the first component of the principal component analysis (Figs. 10a and 10b) excepting for a group of four samples which appear to belong more to the group with grit than to the one without. At this same level of classification efficiency the group of rocky soils is subdivided into three. The distinguishing criteria are primarily the surface rock cover, the amount of grit in the A-horizon, clay in the A- and B-horizons and nutrient status. Those samples with high rock cover and grit appear higher up on the second principal component and those samples with higher clay content and nutrient status appear further to the left on the first principal component (Figs. 10a and 10b).

Further sub-divisions which are evident in the cluster analysis are not described since they are not generally interpretable although the group membership appeared to be determined relatively efficiently. This was tested by subjecting the group classification demarcated by 35% efficiency level on the cluster analysis to the classification routine of canonical variate analysis (Nie *et al.*, 1975). Predicted group membership indicated that only three samples were miss-classified thus indicating a classification efficiency of approximately 97% (i.e. 97% of samples were correctly classified by the hierarchical cluster analysis).

Final group limits and allocation of samples to these groups was only made after considering other factors such as geology, landscape position and soil profile characteristics not included in the numerical analysis (see Appendix 2).

3.4.1.2 Land type/soil relations

Before trying to establish whether any relations exist between land type and soils in Mkuzi, it is worth considering first how some of the other soil forming factors (climate, relief, hydrology, organisms, time and man) might have influenced soil genesis.

Mkuzi is small enough and the climate homogeneous enough for there to be no differentiation of soils on the basis of climate. Relief however, varies to a large extent over the reserve and it is well known (Young, 1976) that the spatial distribution of soil types are related to relief at all scales. In addition relief influences soils indirectly through climate and hydrology and must therefore be considered as having an important modifying influence over geology and land form.

Hydrology, expressed mainly as a function of drainage has a major effect on soil formation and in some instances is dominant over other soil-forming factors (Young, 1976). Profile drainage will affect the leaching of soluble salts, exchangeable bases, silica and sesquioxides. At the extremes of poor drainage, gleying will occur. Although the soils of Mkuzi vary markedly in their drainage characteristics, this is to a large extent accounted for by parent material and relief and for this reason drainage is not considered further.

Time is also considered an important factor in soil genesis. In this analysis, time is to a large extent incorporated into the classification of geological substrate. Thus by looking at relations between land type (which incorporates geology, land form, hydrology and time), actual relief and soil, the major soil forming factors in this restricted area should be accounted for.

The relation between land type, relief (catenal position) and soil was evaluated by plotting the land type designation and catenal position of each sample site on the scatter diagram of samples in axis one and two component space resulting from the principal component analysis of the soils data (Fig. 11). At the positive extremes of each axis there is a one to one matching of land type and resultant soil, indicating the very strong influence of geological substrate on soil formation in these areas. At the interface between the two cretaceous deposits and the overlying Plio-Pleistocene dune cordon sands, which results in the group of duplex soils both to the east and west of the dune cordon, some mixing understandably results. The group of sandy clay loam soils is largely related to the Upper Cretaceous glauconaceous marine sandstone deposits although two recent alluvia lying adjacent to the latter deposits are included (Fig. 11). In addition a number of sites from upland areas of late cretaceous deposits are included presumably reflecting the effect of increased clay eluviation due to their position in the soil catena and their proximity to the cordon sand deposits (Fig. 11).

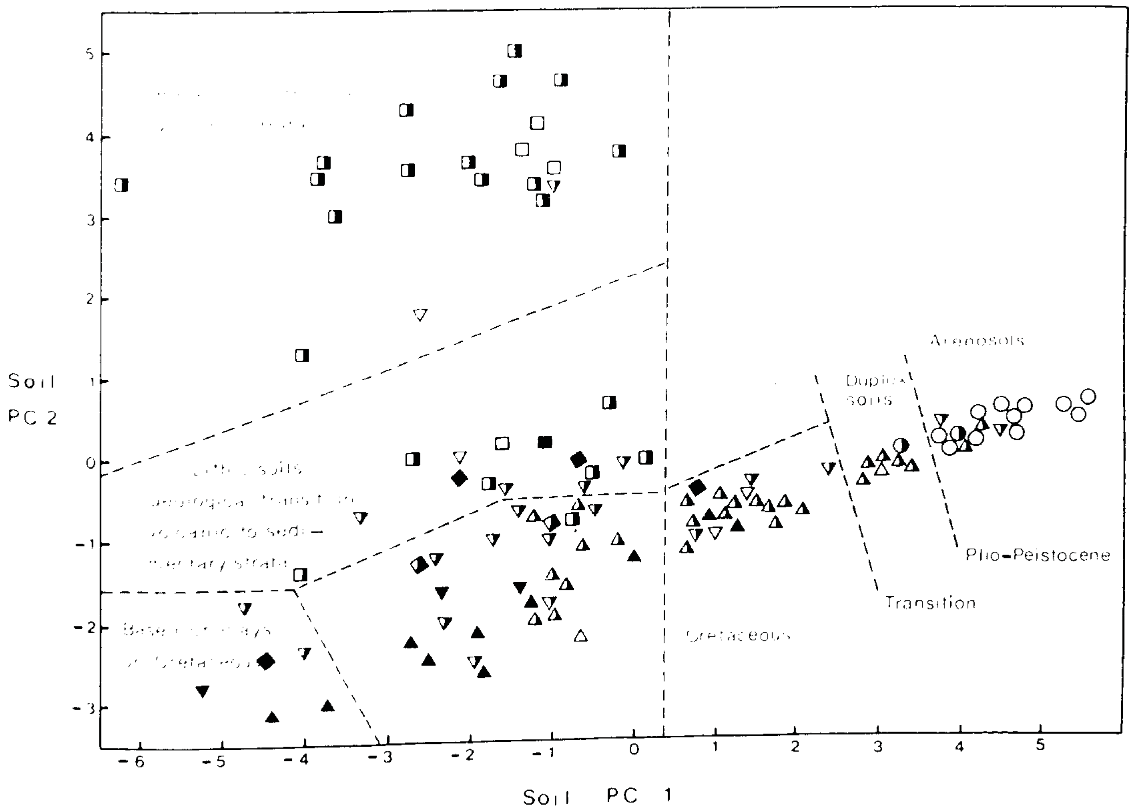

Fig. 11 The relation between land type, relief and soils in Mkuzi Game Reserve. Land type and catenal position plotted in the space defined by the first two components of the soil ordination. Symbols represent:

1) Land Type

◇ Alluvia - Recent (Holocene) and old (Pleistocene - Recent).

○ Orange to red dune cordon sand (Plio - Pleistocene).

△ Glauconaceous marine sandstone (Upper Cretaceous).

▽ Conglomerate, grit, sandstone and siltstone (Lower Cretaceous).

□ Rhyodacite and Rhyolite - volcanic strata (Jurassic).

2) Catenal Position

○ open - crestslope.

◑ half shaded - midslope.

● shaded - footslope and bottom land.

The group of shallow rocky base-rich clay soils (base-rich lithosols) is directly related to the rhyolitic rocks of the Bumbeni and Jozini formations (Fig. 11). An exception is a single sample of early cretaceous conglomerate at the margin of a small plateau which dips fairly steeply down to a small drainage line. The nature of these conglomerates is very loose and rhyolitic in origin and erosive forces have maintained the soil in a shallow raw mineral state very like the upland soils formed on the untransported rhyolite and rhyodacite of the Lebombo Mountains and foot hills.

Although these base-rich lithosols occur as a fairly discrete group on the two dimensional principal component plot (Fig. 11), there is in reality a natural transition from these soils (via a group of lithic soils) to the black, brown and red calcimorphic clays found on the early cretaceous strata. Lithic soils may occur where the weathering volcanic rocks are overlain by a thin veneer of cretaceous sediment and normally on the upland situations of the latter land type or the lower-lying flatter situations on volcanic rocks, where the balance between a reduced erosion rate and weathering has resulted in a lithic soil with a relatively deep (>30 cm) A-horizon over actively weathering rock or saprolite (Fig. 11). Included here also, are some old alluvia consisting generally of shallow and sometimes course stony deposits derived directly from material eroded from the adjacent higher lying volcanic strata.

The group of calcimorphic clays occurring at the negative extremes of the first two principal component axes occur on a mixture of geological strata (Fig. 11). These are characterised by being depositional in origin, but of different chronological ages (Lower Cretaceous, Upper Cretaceous and Holocene). These soils are also characterised by occurring in bottomland situations of the catena and from this I conclude that topography is having a major influence on pedogenesis.

In summary, there are close ties between the underlying geology and soils in Mkuzi. In most instances the nature of the parent material has overriding influence over other soil forming factors. This is especially so for the volcanic strata and dune cordon sands. On parent materials of apparently similar origin (Lower and Upper Cretaceous and Recent Alluvia), although topographic variation is small, it appears to have had a strong influence on soil texture. Furthermore, soil texture has the strongest influence on other soil properties namely structure, consistence, organic matter, cation exchange capacity, moisture retention and drainage (Young, 1976). In addition, the type of clay mineral which has important secondary effects on other soil properties is in this instance influenced primarily by parent material.

Parent material and topography are thus important predictors of soils and have played an important role with other morphological and analytical properties in formulating the soil classification presented in Appendix 2.

3.4.2 Vegetation ordination and classification

3.4.2.1 Determination of sample plot size

The data from nested plots evaluated at two locations in the sandforest and sandveld woodland were summarized as species/area curves for trees and shrubs separately (Figs. 12 and 13). One criterion used as an estimate of minimal area is the point of inflection of the species area curve. However, on examination of the species/area curves it may be seen that the relationships for both the tree and shrub data from the Nkongolwana woodland do not become horizontal or nearly so within the range of measurement and thus could not be used.

A further criterion used, and giving a fairly conservative estimate of minimal area, is obtained where a 10 percent increase in area yields only 5 percent more species (Cain, 1938). These estimates are shown on the species/area curves (Figs. 12 and 13) and are approximately 500, 630 and 410 m^2 for trees in sandforest, shrubs in sandveld and woodland, and shrubs in the sandforest respectively. Once again no estimate could be obtained for trees in the sandveld woodland.

Using the 95 percent criterion (see Mueller-Dombois and Ellenberg, 1974) approximate minimal area estimates of 1200, 780, 1350 and 1150 m^2 for sandveld woodland trees, sandforest trees, sandveld woodland shrubs and sandforest shrubs respectively were obtained. Thus it

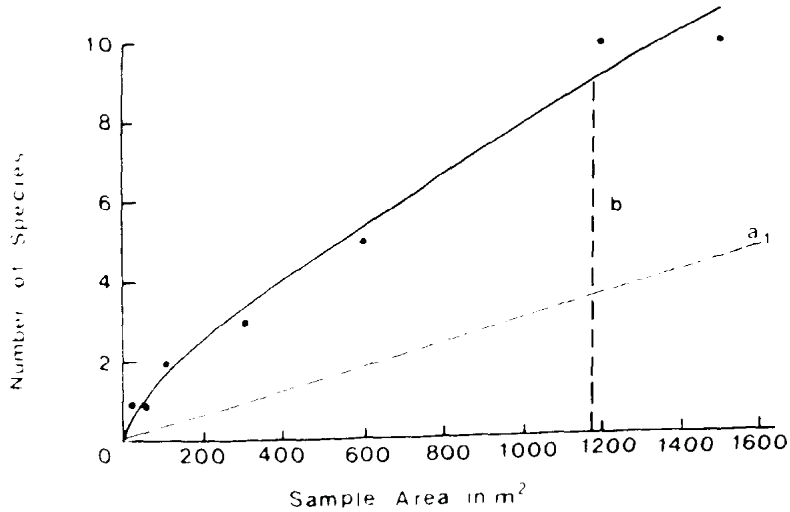

Fig 12a Species area relation for trees in Sandveld Woodland of Nkongolwana. Curve fitted by hand. Minimal area estimate b – using 95 percent criterion. a_1 represents 5 percent increase in species line.

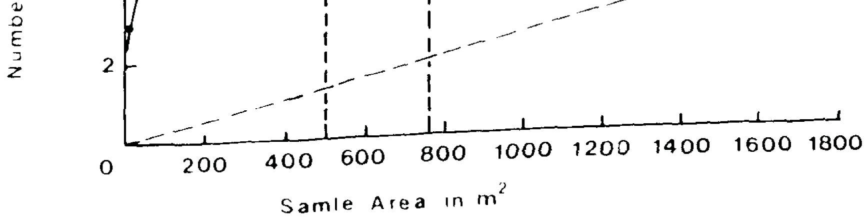

Fig 12b Species area relation for trees in Sandforest of Msinga. Curve fitted by hand. Minimal area estimate using a – 5 percent criterion of Cain(1938) and b – 95 percent criterion. a_1 represents 5 percent increase in species line, a_2 represents tangent parallel to a_1.

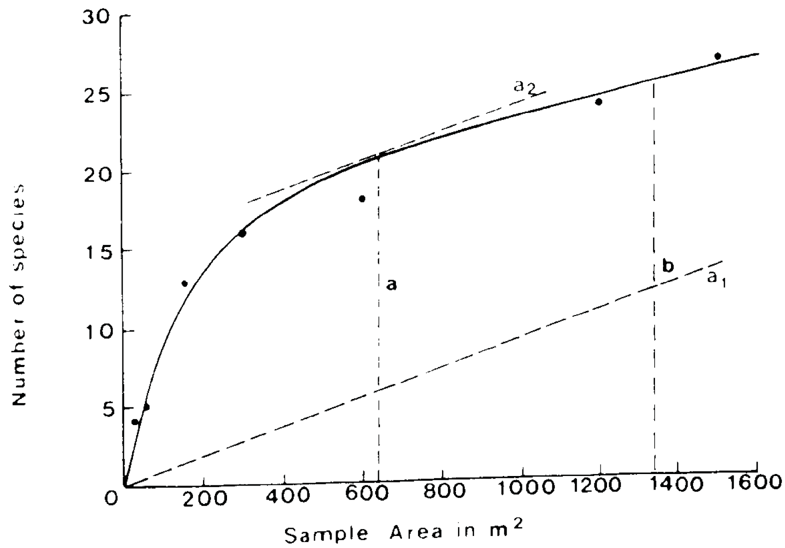

Fig 13a Species area relation for shrubs in Sandveld Woodland of Nkongolwana. Curve fitted by hand. Minimal area estimate using a-5percent criterion of Cain (1938) and b-95percent criterion. a_1 and a_2 as per Fig. 12.

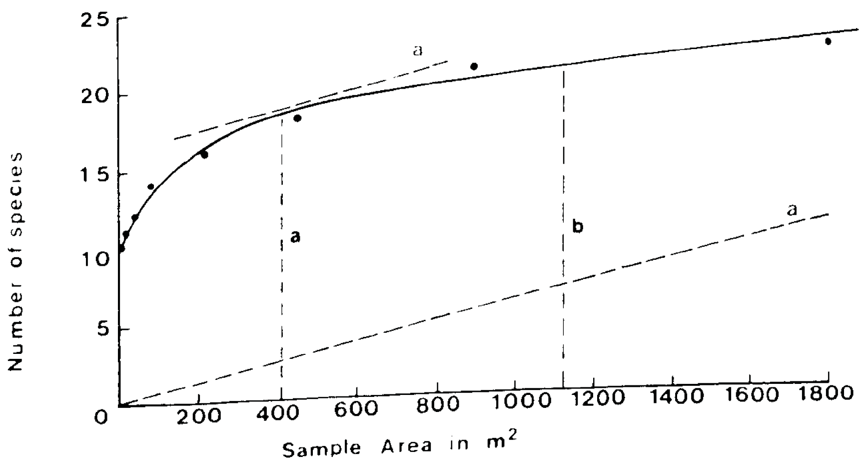

Fig. 13b Species Area relation for shrubs in Sandforest of Msinga. Curve fitted by hand. Minimal area estimate using a-5 percent criterion of Cain (1938) and b-95 percent criterion. a_1 and a_2 as per Fig. 12.

seemed likely that the minimum area for woody plants in these vegetation types could lie somewhere between 410 and 1350 m^2.

For later comparisons with other studies at some stage, it was advisable to select a standard plot size within this range. To this end much American work uses tenth-hectare (20 x 50 m) standard samples (see Whittaker, 1978). For comparative reasons, and since this size (1000 m^2) is within the range of suggested sizes, it was selected for this study.

3.4.2.2 Physiognomic classification

Physiognomic classification of vegetation is generally thought to represent a first level of classification and has been found particularly useful in reconnaissance mapping where the number of species in the area being surveyed is large, or the surveyor is not familiar with the flora (Kuchler, 1967).

Numerous attempts have been made at developing a standard system of physiognomic classification, but understandably these have failed to gain universal usage, probably because different objectives, areas and mapping scales influence the extent to which each vegetation characteristic is emphasized. The needs of this study were that the vegetation classes be easily recognized and mapped from aerial photographs with the minimum amount of ground truthing. This was achieved using the vegetation classification of Greenway (1973) which has relatively broad classes based on the characteristics (density, height and nature of leaf) of the dominant life form. To a lesser extent, and depending on the height and density of the dominating canopy, characteristics of the sub-canopy strata are incorporated.

Each sample was allocated to a "Main Type" and "Type" in Greenway's classification using the physiognomic data collected during field sampling. Once the relation between these and the signature on the aerial photographs had been established, vegetation types and subtypes were delineated on the aerial photo mosaic and then mapped at a 1:50 000 scale.

Six of Greenway's "Main Types" were found in Mkuzi and in all instances his definitions of these were adhered to. Type, and in one instance Subtype, is the lowest hierarchical level to which Greenway's classification is applied as in the lower categories (Subtype and

Association), floristic and environmental factors become distinguishing criteria in the classification. These subdivisions are made in the next section of this study.

The definitions of the physiognomic classes and the allocation of samples to these are presented in Appendix 3. By plotting the physiognomic class assigned to each sample on the first two axes of the soil ordination, relationships between soils and vegetation physiognomy may be examined (Fig. 14). All the woody communities sampled in Mkuzi are considered short or low (less than ten meters tall).

Along the first axis, base poor sands are characterised by semi-deciduous, simple leaved closed woodlands and forest vegetation. As the clay content and general nutrient status increases the vegetation gives way to mixed but mainly simple leaved woodland. The duplex soils are characterised by a mixed but mainly compound leaved woodland and give way to mixed but mainly compound leaved woodland and wooded grassland on the sandy clay loam soils. At the extreme of this gradient, the vertic and melanic calcareous clays are characterised by extremely dense, low thicket and scrub comprising plant species with simple and compound leaves (Fig. 14).

Along the second axis, the gradient from the exposed lithosol of the upper Lebombo Mountains, through lithic soils to the deeper clay soils of the valley bottoms is characterised by a change from grasslands to wooded grasslands to bushland, thicket and scrub. The simple leaved wooded grasslands generally occur on the drier north easterly slopes and the compound leaf wooded grasslands occur on the south slopes, and also increase in importance down the catena (Fig. 14). From these data it would appear that there is no consistent relationship between the ability to withstand dry conditions and either simple or compound leaf form. The first axis (sand to clay gradient) is interpretted as being associated with a decrease in moisture. Simple leaved plants are associated with the moist end of the gradient, compound microphillous plants with the middle, and a mixture of both at the zeric end. On the second axis simple leaved plants occur on north facing (dry) slopes and compound microphillous plants on south facing (moist) slopes. This suggests that it is not

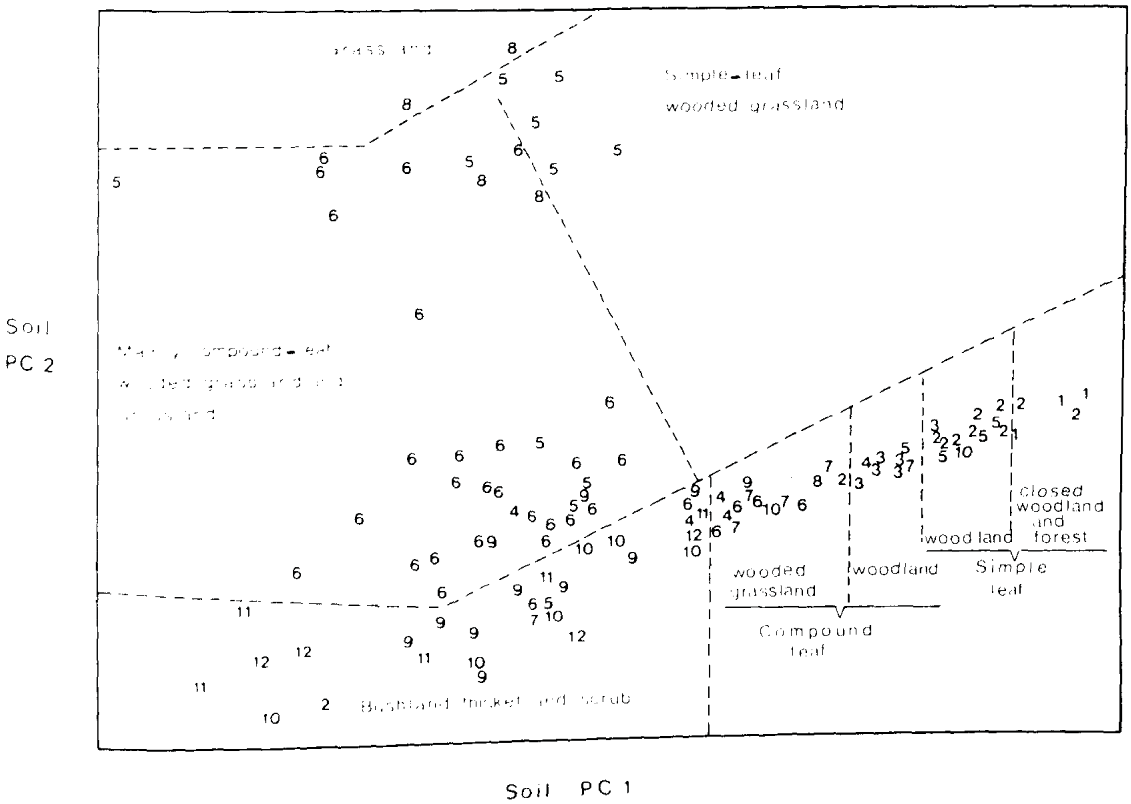

Fig.14 Relation between vegetation physiognomy and soils for each sample. Physiognomic state of each sample is plotted in the space defined by the first two principal component axes of the soils data analysis. Physiognomic groups are:–

1. Simple-leaf closed woodland and forest.
2. Simple-leaf woodland
3. Short compound-leaf woodland.
4. Low compound-leaf woodland
5. Simple-leaf wooded grassland.
6. Short compound-leaf wooded grassland
7. Low compound-leaf wooded grassland
8. Grassland
9. Simple-leaf bushland
10. Compound-leaf bushland
11. Thicket
12. Scrub

the leaf form as such that determines a plants ability to tolerate dry conditions, rather the latter is more likely to be associated with specific mechanisms (e.g. leaf abscission or lowering of transpiration rate) associated with water economy.

3.4.2.3 Floristic ordination and classification

With three data sets (tree, shrub and herbaceous) and a minimum of three analytical techniques (detrended correspondence analysis, two-way indicator species analysis and agglomerative clustering using Orloci's minimum dispersion criterion), there were nine analyses and potentially thirty six comparisons between analyses that could have been made. While all of these comparisons were made it would be too lengthy to present the details of each analysis and comparison. Accordingly, only pertinent information is presented here.

Different sets of data subjected to different analytical procedures will not produce the same result, and a subjective element is therefore introduced in deciding which classification should take precedence over the others. So, although I am primarily concerned with the floristic analysis of vegetation in this section, the level of grouping and the selection of one analysis in preference to others has been influenced to a large extent by environmental considerations.

3.4.2.3.1 Preliminary analysis of woody vegetation

The first analyses were undertaken on tree and shrub data sets separately. Both produced variable but nevertheless interpretable results. However, instead of subjectively integrating the separate tree and shrub classifications into one, it was decided that a more objective solution would be to combine tree and shrub cover-abundance estimates for each sample site into a single estimate and then analyse this combined data set. The results of this analysis would theoretically be more robust than analyses of the individual matrices, having been derived from a matrix containing more species, but fewer zero values. It is possible however, that the resulting classification does not match physical characteristics of the environment as well as the individual classifications, due to the effect recent disturbance might have had on the species composition of the shrub layer.

3.4.2.3.2 Woody plant ordination and environmental interpretation

The first two axes derived from the detrended correspondence analysis of these data show two clear gradients (Figs. 15 and 16). The first axis with a gradient length of 6,46 half changes has species characteristic of sand forest (*Cleistanthus schlechteri, Salacia leptoclada, Croton gratissimus, Hymenocardia ulmoides, Strychnos henningsii, Albizia forbesii, Pteleopsis myrtifolia* and *Dialium schlechteri*) at its positive extreme, and species characteristic of dense bushland and thicket (*Croton menyhartii, Acacia luederitzii, Euclea undulata, Carissa bispinosa, Schotia capitata, Grewia occidentalis, Acacia grandicornuta* and *Sideroxylon inerme*) normally found on heavy clay bottomlands, at the negative extreme.

The second axis has a gradient length of 3,92 half changes and is characterised by species of the higher lying Lebombo foothills (*Acacia karroo, Dombeya rotundifolia, Aloe marlothii, Diospyros lycioides, Acacia caffra, Rhus pentheri, Ormocarpum trichocarpum*, and *Sclerocarya caffra*) at the positive extreme and by species of low lying clay loam soils (*Lippia rehmannii, Maerua edulis, Acacia tortilis, Acacia senegal, Bolusanthus speciosus, Carissa tetramera, Acacia xanthophloea* and *Turrea obtusifolia*) at the negative extreme. The third and fourth axes of 2,92 and 3,47 half changes length are uninterpretable.

To investigate whether the first three axes were at all interpretable in terms of the measured physical parameters, a correlation analysis of sample position along the first second and third axes of the soil and vegetation ordinations was undertaken (Table 3, Fig. 17a and 17b). The first soil axis associates most strongly with the first detrended correspondence analysis axis of vegetation (r^2 = 0,391) (Table 3).

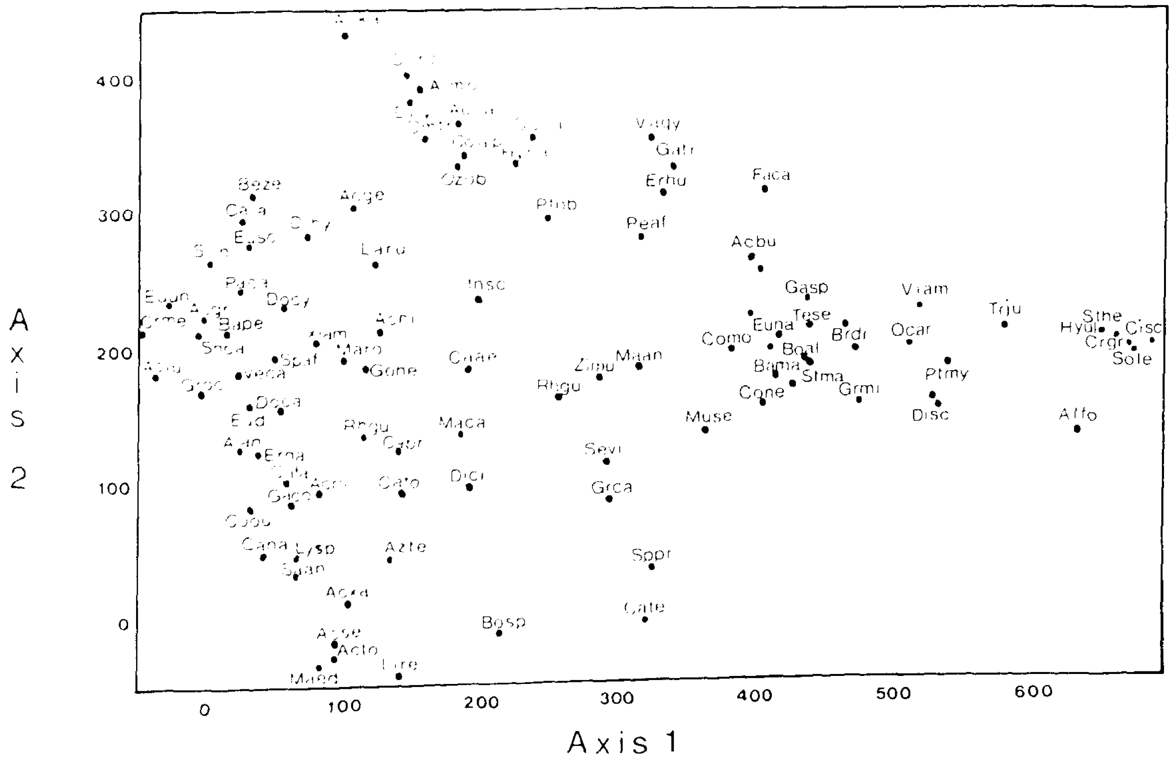

Fig. 15 Detrended correspondence analysis of combined woody plant data (trees and shrubs). Species represented in the space defined by the first two ordination axes. See Table 2 for species name abbreviations.

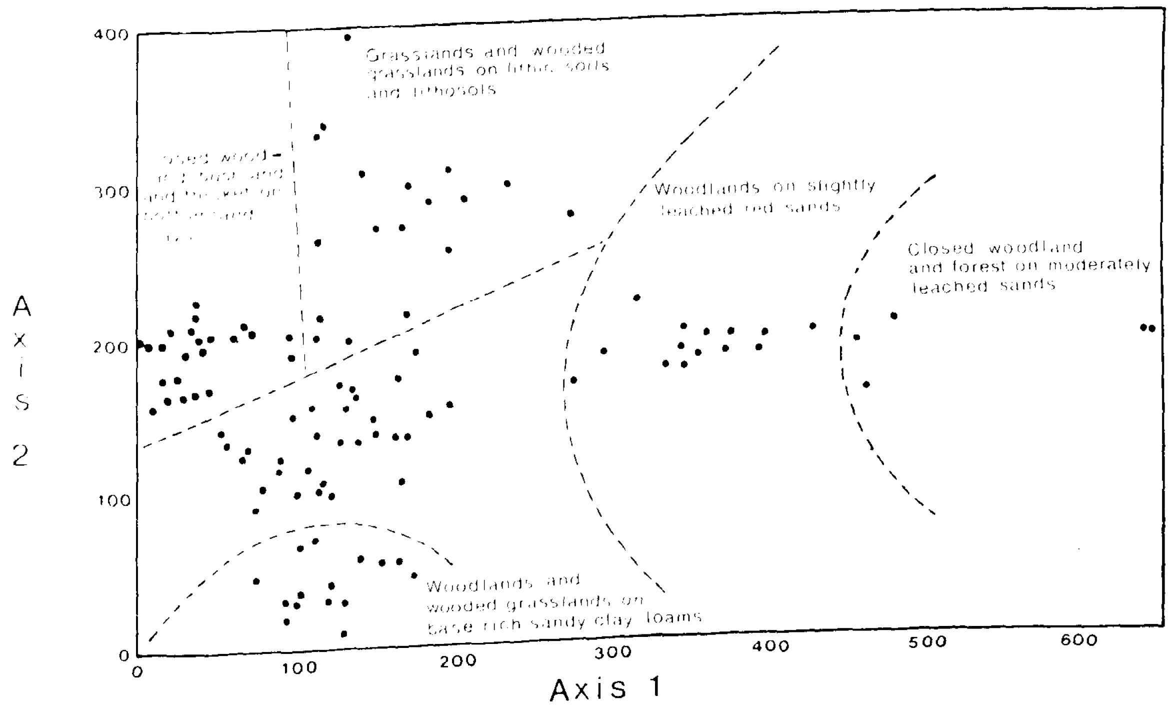

Fig. 16 Detrended correspondence analysis of combined woody plant data. Sample stands represented in the space defined by the first two ordination axes.

able 2. Woody plant names and abbreviations used in figures. Nomenclature is according to Ross (1972).

Abbr.	Name	Abbr.	Name
Acbu	Acacia burkei	Acca	A. caffra
Acge	A. gerrardii	Acgr	A. grandicornuta
Acka	A. karroo	Aclu	A. luederitzii
Acni	A. nigrescens	Acnl	A. nilotica
Acse	A. senegal	Acto	A. tortilis
Acxa	A. xanthophloea	Alan	Albizia anthelmintica
Alfo	Albizia forbesii	Alma	Aloe marlothii
Anmo	Ancylanthus monteiroi	Azte	Azima tetracantha
Bama	Balanites maughamii	Bape	Balanites pedicellaris
Beze	Berchemia zeyheri	Boal	Boscia albitrunca
Bosp	Bolusanthus speciosus	Brdi	Brachylaena discolor
Cana	Cadaba natalensis	Cabr	Capparis brassii
Cafa	Capparis fascicularis	Cato	Capparis tomentosa
Cabi	Carissa bispinosa	Cate	Carissa tetramera
Clsc	Cleistanthus schlechteri	Coap	Combretum apiculatum
Como	Combretum molle	Cone	Commiphora neglecta
Coca	Cordia caffra	Coov	Cordia ovalis
Crgr	Croton gratissimus	Crme	Croton menyhartii
Crps	Croton pseudopulchellus	Disc	Dialium schlechteri
Dici	Dichrostachys cinerea	Dihy	Dinocanthium hystrix
Dily	Diospyros lycioides	Docy	Dombeya cymosa
Doro	Dombeya rotundifolia	Doca	Dovyalis caffra
Ehri	Ehretia rigida	Erhu	Erythrina humeana
Erna	Erythrococca natalensis	Eudi	Euclea divinorum
Euna	Euclea natalensis	Eusc	Euclea schimperi
Euun	Euclea undulata	Euca	Eugenia capensis
Faca	Fagara capensis	Gatr	Galpinia transvaalica
Gaco	Gardenia cornuta	Gasp	Gardenia spatulifolia

Table 2 cont.

Abbr.	Name	Abbr.	Name
Gohe	Gossypium herbaceum	Grca	Grewia caffra
Grmi	Grewia microthyrsa	Groc	Grewia occidentalis
Hyul	Hymenocardia ulmoides	Hyna	Hyphaene natalensis
Insc	Indigofera schimperi	Laru	Lantana rugosa
Laca	Lasiocorys capensis	Lire	Lippia rehmannii
Lysp	Lycium sp.	Maan	Maerua angolensis
Maca	Maerua cafra	Maed	Maerua edulis
Maro	Maerua rosmarinoides	Muse	Mundulea sericea
Ocar	Ochna arborea	Ocna	Ochna natalitia
Omtr	Ormocarpum trichocarpum	Ozob	Ozoroa obovata
Paca	Pappea capensis	Peaf	Peltophorum africanum
Phma	Phyllanthus maderaspatensis	Ptob	Ptaeroxylon obliquum
Ptmy	Pteleopsis myrtifolia	Puve	Putterlickia verrucosa
Rhdi	Rhoicissus digitata	Rhrh	Rhoicissus rhomboidea
Rhtr	Rhoicissus tridentata	Rhgu	Rhus gueinzii var. spinescens
Rhal	Rhynchosia albissima	Sale	Salacia leptoclada
Saan	Salvadora angustifolia	Scbr	Schotia brachypetala
Shca	Schotia capitata	Scca	Sclerocarya caffra
Sevi	Securinega virosa	Siin	Sideroxylon inerme
Sppr	Sphedamnocarpus pruriens	Spaf	Spirostachys africana
Sthe	Strychnos henningsii	Stma	Strychnos madagascariensis
Stsp	Strychnos spinosa	Tese	Terminalia sericea
Trju	Tricalysia junodii	Tuob	Turraea obtusifolia
Vacy	Vangueria cyanescens	Veca	Vepris carringtoniana
Viam	Vitex amboniensis	Xeob	Xeromphis obovata
Xeru	Xeromphis rudis	Xiam	Ximenia americana
Zimu	Ziziphus mucronata		

Table 3. Coefficients of determination (r^2) between sample position on the first four principal component axes of soils and the first three detrended correspondence analysis axes of woody vegetation.

Soil	Vegetation Axis		
Axis	1	2	3
1	0,3907	0,0324	0,0431
2	0,1080	0,2267	0,0098
3	0,0431	0,0210	0,0281
4	0,0003	0,1024	0,0281

From this we may conclude therefore that the first major soil gradient (primarily a gradient from moderately leached acid sands to base rich clays) accounts for approximately 39 percent of the variance in the first vegetation ordination axis. As may be seen (Fig. 17a) the relation is more curvilinear than linear, with small inconsistant changes in vegetation occurring at the base rich clay and clay loam end of the soil gradient. Large consistent changes in the species composition, however occur with only small changes in the soil gradient at the sandy moderately leached end of the latter gradient.

Since only top soils were analysed and included in the soil ordination, we might expect the duplex soils to be anomalous when investigating woody plant responses to soils, as deeper rooted woody plants are likely to reflect subsoil characteristics to a larger degree than topsoil characteristics. This appeared to be the case (Fig. 17a) since on the exclusion of the duplex soils from the correlation analysis, the variance in the vegetation accounted for by the first soil ordination is increased from 39 percent to 47 percent (r^2 = 0,466).

The second soil principal component axis associates most strongly with stand position along the second detrended correspondence analysis

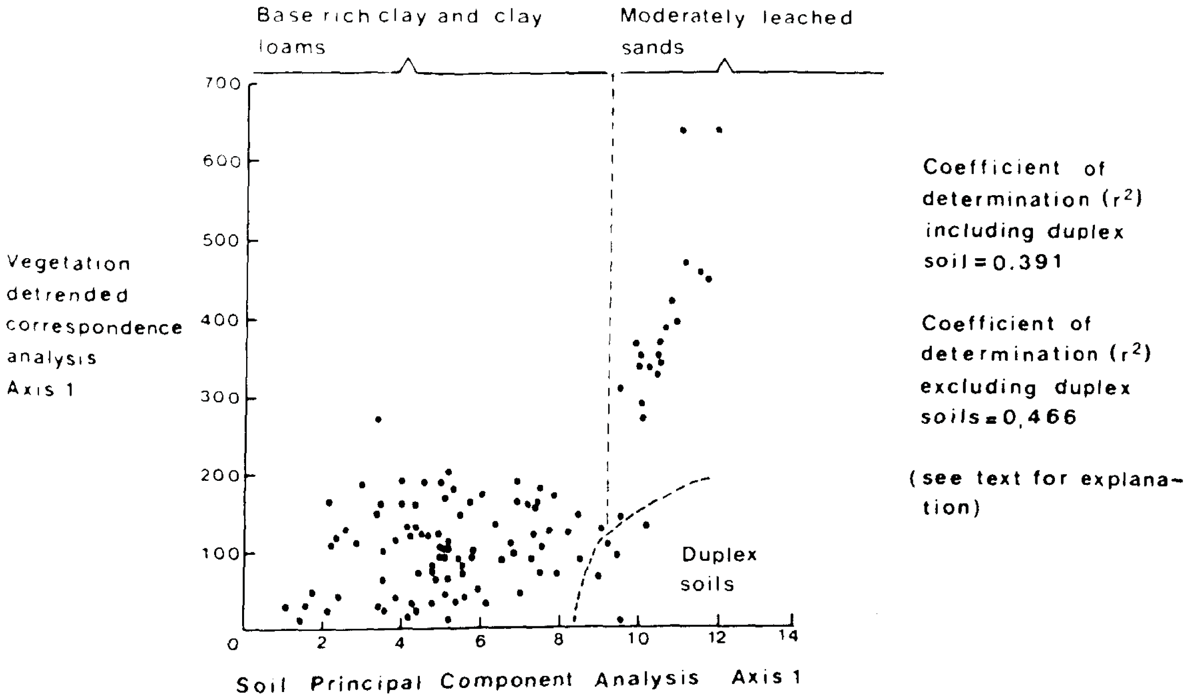

Fig. 17 a Relation between sample position on, the first principal component axis of soils and the first detrended correspondence analysis axis of vegetation.

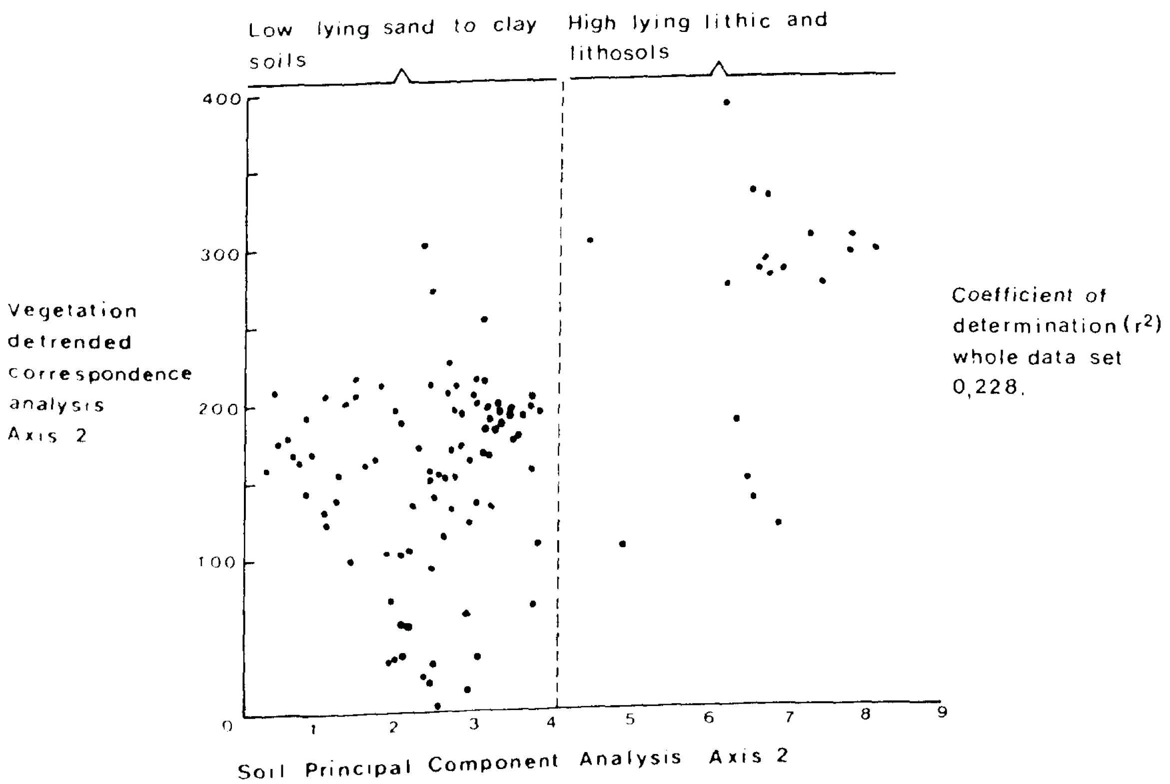

Fig. 17b Relation between sample position on, the second principal component axis of soils and the second detrended correspondence analysis axis of vegetation.

axis of vegetation and has a coefficient of determination of 0,227 (Table 3, Fig. 17b). Thus only 23 percent of the variation in vegetation along this axis is explained by the soil gradient, which is primarily one from highlying, shallow well-drained lithosols to lowlying deep but poorly drained clays. By contrast the third soil axis, although it is most strongly associated with the third vegetation axis, accounts for only 7 percent of the variation and cannot be interpreted in terms of this axis.

To investigate these relationships further, sample position along the first vegetation ordination axis is plotted against various environmental parameters, namely percentage clay in the A-horizon, available water capacity, profile available moisture (see Appendix 4 for the derivation of these two variables), and total exchangeable bases (Fig.'s 18a, 18b, 18c and 18d). There is a general decrease in the amount of clay from the one end of the vegetation gradient to the other (Fig. 18a). However, plants cannot respond to clay per se but to nutritional and soil/water characteristics which are to a large extent a function of the clay content of the site. The plot of available water (the simplest measure of moisture regime) showed a very similar pattern to that obtained with A-horizon clay (Fig. 18b). In both cases the duplex soils have been displaced to the lower left corner of the graph, a misrepresentation due to the emphasis given to the low clay content of the A-horizon.

The plot of profile available moisture against the first vegetation ordination axis (Fig. 18c), does not improve on the last relation. Instead, the lithosols and lithic soils become apparent with very low profile available moistures and occur slightly left of centre on the vegetation ordination axis. From this it appears that the first ordination axis is not directly related to a moisture gradient in any simple way.

The plot of total exchangeable bases against stand position on the first vegetation ordination axis (Fig. 18d) resembles quite closely the same relation but with clay percentage on the ordinate. Indeed clay content, intensity of leaching and exchangeable bases are all

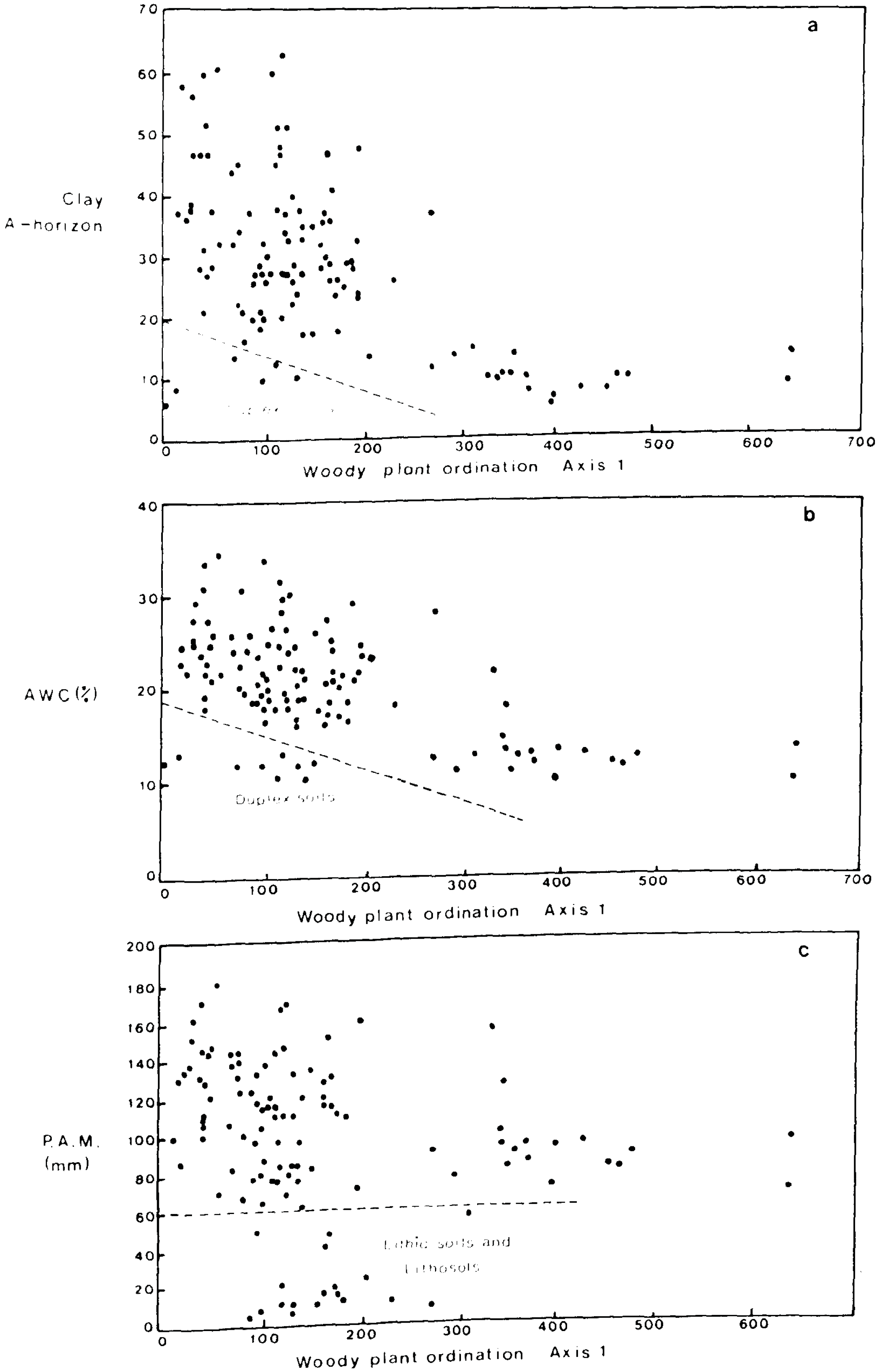

Fig. 18. Relations between a) A-horizon clay, b) available water capacity (A.W.C.), c) profile available moisture (P.A.M.) and sample position on the first woody plant ordination axis.