AUTOMATIC CLASSIFICATION AND ECOLOGICAL PROFILES OF SOUTH - WESTERN TRANSVAAL HIGHVELD GRASSLAND

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ABSTRACT

A quantitative, semi-detailed plant ecological study of the area between 25° 54' and 26° 22' E and 26° 00' and 26° 20' S, situated around the town of Lichtenburg in the South-western Transvaal, South Africa, is reported. Mean annual temperature of the study area is 17 °C and annual rainfall is about 600 mm. A basic difference is recognised between the Bankenveld Land System and the CT Grassland Land System. The former is underlain by dolomite with lithosolic soils, Bankenveld vegetation and cattle ranching as the chief land-use, whereas the latter is underlain by granite, Ventersdorp lavas, Dwyka tillite and surface limestone with Shorrocks, Mangano and Lichtenburg series soils, Cymbopogon-Themeda Veld vegetation and extensive cultivation of maize as the chief land-use.

One hundred and ten 16 m^2 quadrats were placed within each Land System by means of a stratified-random strategy. Of the 247 species encountered, nearly 100 occurred in less than six quadrats. Themeda triandra, Aristida congesta, Elionurus argenteus, Anthospermum rigidum and Justicia anagaloides were common throughout. Two association analyses (AANAL) were carried out and a total of 21 final groups were described and 11 groups were mapped at 1:50 000. In addition, Bankenveld Land System quadrats were classified by divisive information analysis (DIVINF) and AXOR (axis ordination) and results were compared with those of AANAL. Results were basically similar although AANAL was sensitive to the number of species recorded in each quadrat and the other two techniques were not.

Various methods of data reduction were applied to Bankenveld Land System quadrats and AANAL and DIVINF were used to classify the resulting data. Even rather severe data reduction was found to have little effect on the groups produced or on the configuration of the hierarchy when either statistical methods or ecological interpretation were used to compare groups.

The Ecological profiles technique was successfully applied to the Bankenveld Land System data. Although the data were not entirely suitable in this study it was concluded that the technique has great value as it can provide the kind of information needed to explain the ecology of common South African plant species.

Finally, some proposals for future semi-detailed surveys were made. The basic stratified-random sampling strategy was found acceptable but would be improved by choice of a sample site representative of the physiognomic-physiographic unit being sampled. For optimal results, the groups resulting from an automatic classification will have to be refined, possibly by means of the Braun-Blanquet table method.

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CHAPTER 1

I N T R O D U C T I O N

The plant ecology of the natural and semi-natural vegetation of part of the Highveld Agricultural Region is being studied by the writer as a project by the Botanical Research Institute for the Department of Agricultural Technical Services, Pretoria, South Africa. This thesis reports on the results of a quantitative ecological study of the Lichtenburg area, which falls, together with the Maquassie area, under the writer's responsibility for the western section of the Agricultural Region. J.C. Scheepers(1), working in collaboration with the writer, is responsible for the eastern section of the Region, including the Kroonstad, Bethlehem and Villiers areas.

The overall model for the Highveld Region Survey was drawn up by Scheepers in collaboration with D. Edwards(2). The writer

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became involved with the Survey towards the end of the preliminary planning phase. Instead of spreading surveying efforts equally over the whole Region of approximately 11 655 000 ha (45 000 sq miles), it was decided to opt for the Key Area approach whereby surveying efforts would initially be concentrated in the Lichtenburg, Maquassie, Kroonstad, Bethlehem and Villiers Key Areas. Responsibility for surveying Key Areas was assigned as stated above. Each Key Area is a quarter degree square, covering approximately 69 000 ha (270 sq miles). Surveys of Key Areas are to be followed by extrapolatory surveys linking all five Areas. The basic sampling strategy of 4 by 4 m quadrats, with a stratified-random distribution was chosen during preliminary studies for the Kroonstad Key Area and the Lichtenburg survey reported here followed suit to aid later comparison and extrapolation.

Two basic Land Systems (Dowling 1968, Mabbutt 1968), which may be equated with bioclimatic regions(3) or subregions(4), occur in the study area. Throughout this account they are

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(3) Defined by Phillips (1973) p. 30 as: "A bioclimatically natural unit of extensive area, often constituted by a number of ecologically-related smaller units - the subregions - either forming portion of the same great area or, more often, widely separated by other bioclimatic units".

(4) Defined by Phillips (1973) p. 30 as: "A constituent of the bioclimatic region".

referred to, for convenience and brevity, as CT Grassland and Bankenveld Land Systems. The former includes Dry *Cymbopogon-Themeda* Veld and Sandy *Cymbopogon-Themeda* Veld and the latter covers part of Bankenveld (Acocks 1953). The main features of and differences between the two Land Systems are detailed in Chapter 2. Briefly, Bankenveld lies on an area of dolomitic lithosol north of Lichtenburg where a great deal of the natural and semi-natural vegetation (physiognomically a grassland) remains and the main land-use activity is cattle and sheep farming. CT Grassland is an extensively-cultivated area south, east and west of Lichtenburg where maize is the chief crop. Natural and semi-natural vegetation is rare but, where still encountered, the physiognomic structure is grassland or savanna. In general, it is only small rock outcrops and poorly-drained areas which are not ploughed in the CT Grassland Land System.

With regard to this study area, it is Bankenveld which should receive most attention from plant ecologists and agricultural officers interested in natural pastures because the remnants of natural vegetation in CT Grassland are unrepresentative of the bulk of what used to be present there. Emphasis is reversed in soil surveys where most interest is in arable land and Bankenveld is dismissed by pedologists as a lithosol (see: Van der Bank 1968).

The aims of the present survey were the production of a vegetation map at a scale of 1:50 000 and an account of the plant ecology of the Lichtenburg Key Area, referred to throughout this account as the "study area". In Chapter 3, the vegetation sampling strategy is described and the vegetation classifications produced by straightforward association analyses of both Land Systems are given.

Chapters 4, 5 and 6 are concerned with the use and testing of advanced methods of automatic classification, including AXOR (axis ordination) and divisive information analysis as well as the use of a French synthesis technique, Ecological profiles, on the vegetation of the Bankenveld Land System. As the data were gathered primarily for a rapid, semi-detailed survey of the vegetation of the Lichtenburg area, the data were generally inadequate, or at least not optimal for most of the newer methods of classification which were applied. Results in these Chapters are therefore intended to indicate the utility of the particular method and ecological results are preliminary. Nearly all computations were undertaken while the author was overseas (see: Morris 1973), making use of computer programs that are not available in South Africa.

Some thoughts on future strategies in semi-detailed botanical surveys in South Africa are given in Chapter 7, in the light of results from the present study. Conclusions with regard to the applicability of advanced classificatory techniques in such surveys are also made.

CHAPTER 2

DESCRIPTION OF STUDY AREA

LOCATION AND COMMUNICATIONS

The location of the area studied for the present account and its position relative to towns in the South-western Transvaal, South Africa are indicated in Fig. 1. Initially, the study area

INSERT FIG. 1

was the 2626AA quarter degree square but as parts were very extensively cultivated the area was enlarged westwards to 25° 54' longitude, eastwards to 26° 22' and southwards to 26° 20' latitude to enable placement of enough sampling points in relatively undisturbed vegetation. A rectangular shape was retained even though much of the enlarged area was not sampled. The quarter degree square covers about 69 000 ha (270 sq miles) and the enlarged area about 177 000 ha (680 sq miles).

The town of Lichtenburg is situated near the centre of the 2626AA quarter degree square. Coligny, south-east of Lichtenburg, is the only other town in the study area. Lichtenburg is connected with the surrounding centres of Mafeking, Zeerust, Koster, Coligny, Ventersdorp, Wolmaransstad and Delareyville by tar roads. A good network of gravel roads covers the intervening areas. Lichtenburg is about 200 km (125 miles) west of Pretoria.

The only railway in the area is that between Lichtenburg and Coligny. The line is a branch of the Johannesburg-Kimberley line, passing through Coligny.

CLIMATE

Introduction

Apart from precipitation records and air temperature measurements, no climatic data are available from within the study area. Data from Potchefstroom, and even Pretoria, are used to complete the description of climate given below. Where data from outside the study area are used, they are intended as indications of conditions prevailing within the area and no more. It is considered better to give values, which are assumed to be in the same order of magnitude as those within the study area, rather than none at all. Where observations have been made at more than one meteorological station, as with rainfall, the variability between stations becomes apparent and should be borne in mind when data from only one station are available.

With the exception of Pretoria, the locations of all meteorological stations discussed in the text and listed in Tables are marked on the locality map (Fig. 1).

Radiation and temperature

1) Radiation

Few meteorological stations in South Africa record radiation. The station nearest to Lichtenburg is at Pretoria, half a degree further north and 200 km east. The instrument in Pretoria is a Kipp solarimeter and all measurements are from a horizontal surface. Although it is unwise to extrapolate so far, the figures for Pretoria indicate the magnitude of the values at Lichtenburg. As the principal factor controlling radiation is latitude, use of the Pretoria station cannot lead to gross errors in extrapolation to the South-western Transvaal. It is likely that radiation received at the surface of the earth in the South-western Transvaal is higher than that at Pretoria as the amount of rainfall is less and therefore cloudiness, which influences radiation inversely, is also less. There are, however, no measurements to quantify the increase.

It is well known (Schulze 1965) that the annual march of radiation at a point on the earth's surface is that received at the outer limit of the atmosphere, attenuated by factors which absorb, scatter and reflect incoming radiation. The percentage radiation received at the top of the atmosphere, but not reaching the surface of the earth at Pretoria, averages 39 percent annually with a maximum attenuation of 45 percent in December and minimum of 31 percent in June.

The monthly march of radiation at Pretoria is given in Table A1[5]. The highest mean daily sums occur in summer from October to February when the global radiation exceeds 530 $cal/cm^2/day$ and the lowest mean daily sums in June and July (less than 360 $cal/cm^2/day$). Radiation increases sharply from July to September and then stays fairly constant during summer before starting to decrease in February. The levelling off of radiation in summer is due to an increase in cloudiness compensating for radiation increases during this season. Diffuse radiation varies from over 150 $cal/cm^2/day$ in summer to less than 80 $cal/cm^2/day$ in winter. The highest sum of radiation recorded on a single day (800 cal/cm^2) occurred during the month of January and the lowest (27 cal/cm^2) during July.

Mean hourly sums of global and diffuse radiation for January, March, May, July, September, November and the year are given in Table A2. In summer, higher radiation is usually received during the morning hours than during the afternoon while in winter the distribution is almost perfectly symmetrical. This suggests that during summer, cloudiness, which reduces radiation, is more prevalent during the afternoon.

As the study area is generally flat, the influence of increased or decreased insolation on sloping ground, as discussed recently by Schulze (1970) and Downing (1972), is of little importance.

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(5) Climatological Tables A1 to A14 are given in an Appendix.

2) Sunshine and cloudiness

The nearest meteorological station recording sunshine duration is Potchefstroom, 120 km south-east of Lichtenburg. The monthly and daily marches of sunshine follow interesting trends when compared with the march of radiation.

Average monthly and annual sunshine duration in hours at Potchefstroom is given in Table A3. During winter months from May to September over 80 percent of the theoretical maximum sunshine is recorded while in summer the amount drops to about 65 percent. The average number of sunshine hours per day stays remarkably constant through the year with a slight peak in winter, when day-length is shortest. The phenomenon can be explained by the greater amount of cloud cover present during summer which more than cancels out the effect of longer days. On most days, over 50 percent of the theoretical maximum is recorded and the number of days with no sunshine, or one to 10 percent of the possible maximum, are few.

Mean monthly sunshine duration for each hour is given in Table A4. As is observed with global radiation, the amount of sunshine recorded during the morning is markedly greater than that recorded during the afternoon in summer but sunshine is equitably spread through the day during winter. This indicates once again that more cloud is usually present during the afternoons in summer while clouds (when they occur) are equally spread through the day in winter.

Very little data on cloudiness are available according to Schulze (1965). He suggests that as cloudiness is recorded only twice each day, at 0800 hours and 1400 hours, if at all, the records cannot be of much value. More can be inferred about cloudiness from hourly radiation and sunshine records than from such sparse observations.

3) Air temperature

Temperature fluctuations in South Africa are summarised by Schulze (1960). Air temperature data (Table A5) have been recorded at Lichtenburg since 1905. Observations until 1950 are the most recently published statistics.

Mean of daily maximum temperature varies from over 28 °C in December and January to under 20 °C in June and July. Mean of daily minimum is about 15 °C in January and February and less than 2 °C in June and July. Of more interest ecologically are the extreme maxima and minima (Walter & Leith 1960). Extreme maximum temperatures in summer (September to February) exceed 35 °C while in winter the maximum recorded temperatures exceed 25 °C (July). Extreme minima as low as -10 °C have been recorded in July while minima below -5 °C have occurred from May to August. In mid-summer (December to February) the extreme minimum temperature is above 3 °C.

4) Grass minimum temperature and frost

Grass minimum temperatures are available for Potchefstroom and are summarised in Table A6.

Mean grass minimum temperature varies from 11 °C in December, January and February to below -5 °C in June and July. The maximum exceeds 16 °C from November to March and drops to 8 °C in July while the minimum temperatures throughout the year (except February) are below 1 °C. The extreme minimum of -17 °C is recorded during July.

In the absence of observations on frost occurrence, climatologists have used various air temperatures to indicate the occurrence of frost. If the criteria of the publication Weather Bureau (1954), namely a minimum temperature less than 0 °C in a Stevenson screen 1,2 m above the surface, are accepted, Lichtenburg averages 106 days per annum (30-year records) with a possibility of experiencing frost. The average first date is 19th May and the average last date is 2nd September. As the average number of days on which frost actually occurs is 26, frost may be expected one night in four from the middle of May until the end of August. The extreme first date was 16th April and the extreme last date on which frost has been recorded was 26th September.

5) Soil temperature

Soil temperatures have been recorded at Potchefstroom for five years. Mean monthly soil temperatures at five depths at 0800 hours and at two depths at 1400 hours and 2000 hours are given in Table A7. As soil temperatures at 60 cm and 120 cm do not vary by more than about 1 °C through the day only the temperatures recorded at 0800 are given for these depths.

The annual march in soil temperature from high in summer to low in winter is evident from Table A7. At 60 cm and 120 cm the annual range is much smaller than it is nearer the surface. A number of other gradients are also clear. At 0800 hours from September to March temperature increases with depth to 60 cm and then decreases slightly by 120 cm. During winter months (April to August), temperature increases with depth to 120 cm. As expected, surface layers of soil are warmer at 1400 hours and 2000 hours than at 0800 hours through absorbing radiation. The differences between temperatures at 1400 hours and 2000 hours are small, however, with the 1400 hours reading being slightly higher at 10 cm and slightly lower at 20 cm throughout the year.

The highest monthly mean temperatures have been recorded at 1400 hours in November, December, January and February when the temperature exceeded 29 ^{o}C at 10 cm and 24 ^{o}C at 20 cm. The lowest temperatures in June and July at these depths, where most plant roots are located, were 8,3 ^{o}C at 10 cm (0800 hours) and 10,2 ^{o}C at 20 cm.

Surface wind

No information on surface wind is available from within the study area but the general features may be determined from a knowledge of air circulation patterns over South Africa and from observations of wind speed and direction at nearby meteorological stations. In general, there seems to be little seasonal change in wind direction or force. Winds with a northerly component predominate but it is difficult to assign any one prevailing direction according to Schulze (1965). The northerly component results from the normal anticyclonic circulation of air around a high pressure cell located over the interior of South Africa throughout the year. Apart from a weakening and southward movement of the system through a few degrees of latitude in summer, the essential features of the circulation in winter and summer are not greatly different (Tyson 1969). Although a wind-rose diagram for Potchefstroom is given in Weather Bureau (1960b), it is not presented as mean wind direction in an anticyclonic system may change over short distances and is therefore unlikely to represent the situation at Lichtenburg adequately.

The strongest winds do not necessarily coincide in direction with the prevailing, or most frequent, winds. This is particularly true here, according to Schulze (1965). Winds from the south-westerly sector, although infrequent, are often the strongest. Such south-westerly to southerly winds of short duration are almost always associated with thunderstorms.

Precipitation

Precipitation within and near the study area is almost entirely in the form of rain, most of which falls during summer. While severe hail storms are experienced occasionally, snow is rare and is not discussed further. Data from a number of meteorological stations measuring rainfall within and near the study area are given in Tables A8 and A9. Although there are variations in temperature and other climatic variables through the study area, these cannot be studied since rainfall is the only statistic for which more than one set of values are available for the study of variation. All the data are presented to show variability and rainfall gradients through the area and its surround.

Mean annual rainfall at Lichtenburg is just over 600 mm, with 85 percent falling during the six summer months from October to March. Within the study area, annual rainfall varies from 550 mm to 625 mm while in the surrounding area it varies from a minimum of 566 mm at Mafeking (to the west) to a maximum of 654 mm at Koster (to the north-east). At Lichtenburg, the month with peak rainfall is January, with an average of over 100 mm, while June, July and August are driest with less than 10 mm each. The rainy season usually starts in October and the monthly total increases steadily until January after which it falls gradually until April and May.

Rain may be expected on ten days each month during December and January and on only one day per month in winter (Tables A8 and A9). Rain is recorded on about 60 days per year at Lichtenburg. The number of rain-days per month and year are important for judging the distribution of rainfall; whether it falls in many showers or as a few downpours. According to Schulze (1965) the bulk of rainfall results from thunderstorms and instability showers. The data given in Tables A8 and A9 and personal observations within the area confirm that a major part of the rain does fall in heavy downpours.

Variation in rainfall from one station to the next, even when these are in close proximity, will be obvious from examination of the tables. Weather Bureau (1960a) considered that as even neighbouring stations showed widely divergent tendencies in long-period averages it was not only difficult, but also misleading, to use data from a few separate stations to make deductions about rainfall over larger areas. They considered that a greater measure of reliability was obtained, particularly with regard to problems such as long-term agricultural planning, by forming a parameter, namely district rainfall, which could then be used for further analysis. In 1934, Schumann & Thompson recognised 32 rainfall districts but a more satisfactory division was made later by Schumann & Hofmeyr (1938). The Lichtenburg study area falls on the boundary running north to south between Districts 19 (to the west) and 21 (to the east) in Schumann & Hofmeyr (1938) and Weather Bureau (1960a) and within District 84 in Van Rooy (1972). Mean monthly rainfall for these three districts is summarised in Table A10.

The trend of increasing aridity to the west is evident from figures for Districts 19 and 21. Rainfall data for District 84 (Table A10) agree well with data for Lichtenburg (Table A8) although the mean annual rainfall is 10 mm less and the summer monthly peak is also not as high for the District as for the town. In District 84 75 percent of the precipitation is recorded during the five months from November to March.

Some data on the occurrence of droughts and the variability of rainfall are available. Weather Bureau (1960a) tabulated the frequency of droughts of different duration for each rainfall district (Table A11) for twelve monthly precipitations below

75 percent of the annual rainfall. The Table shows that the area is subjected to some particularly critical and harmful droughts on account of their lengthy duration (Weather Bureau 1960a).

Schumann & Mostert (1949) developed a relationship (V) as a measure of rainfall variability:-

$$V = \frac{1}{nM} \sum_{i=1}^{n} \left| p_i - M \right|$$

where p_i is the individual amount for year i, M is the mean district rainfall and n is the number of years. Measure (V) is equal to zero when annual rainfall is precisely the same and it has a maximum value of two. Values for V in Districts 19 and 21 (Schumann & Hofmeyr 1938) are given in Table A12. The variability within both Districts is similar. The maximum variability throughout the country is found in District 21, in June, while the variability in District 19 is also high in June. In January the variability is much lower and over the whole year it is fairly low.

Schumann & Mostert (1949) devised a coefficient for rainfall reliability (R) as:-

$$R = \left(1 - \frac{V}{2}\right)^2$$

where R attains its maximum value of unity when V equals zero. Values for R in January, June and the year are given in Table A12. The lowest reliability in the country is found in District 21 in June and the value for District 19 is not much higher. Reliability in January and for the year is much better.

From variability, reliability and drought frequency data it may be concluded that prolonged droughts are a feature of the climate and that variability of winter rainfall is high and reliability low. These conclusions are borne out by maps presented by Schulze (1965) showing that rainfall at Lichtenburg may be 175 percent greater than or 60 percent less than the average. Rainfall for District 84 may be 148 percent greater than or 68 percent less than the mean (Table A10).

The development of squall lines, leading to the formation of cumulonimbus clouds and thunderstorms, the major source of rain, are described by Tyson (1969). He describes shower belts, which contribute to rainfall, as well. He concludes his account of air circulation and precipitation over South Africa by stating that circulation and precipitation cannot be explained in terms of prevailing winds and rigid precipitation types. Instead, South Africa's rainfall must be explained in terms of prevailing vertical temperature gradients and weather systems likely to produce convergence and the ascent of air.

Evaporation

Evaporation from an A-class pan has been recorded for 4½ years at Potchefstroom (Schulze 1965). Although the period is short, results give an indication of the evaporation pattern. Of the average annual evaporation (2140 mm), 32 percent occurred in summer (December to February), 21 percent in autumn (March to May), 16 percent in winter (June to August) and 31 percent in spring

(September to November). The lowest mean monthly evaporation was recorded in June (35 mm) while an average of over 90 mm occurred during each month from October to January.

Vapour pressure and relative humidity

Vapour pressure and saturation deficit have been recorded at Potchefstroom at 0800 hours and 1400 hours (Weather Bureau 1954). Saturation deficit is a measure of the drying power of the air and is the difference between vapour pressure and saturation vapour pressure. In the morning, vapour pressure varies from about 15 mb in summer to 6 mb in winter while the saturation deficit varies from over 9 mb in early summer to less than 3 mb in winter (Table A13). Therefore, the air has three times as much drying power in summer as in winter. The early afternoon vapour pressures are slightly lower than the morning values in summer and are approximately the same in winter while the saturation deficits are much higher in the early afternoon than in the morning, with the same seasonal trend.

Relative humidity has been measured hourly at Mafeking for two years (Table A14). As the recording period is very short the data can only be used as an indication of the relative humidity régime.

In the morning (0600 hours), relative humidity varies from over 80 percent in late summer (January to May) to less than 60 percent in September. At midday, relative humidity is lower than in the morning and the lowest values are recorded in the afternoon at 1500 hours. The lowest mean monthly relative humidity is 21 percent (August) at 1500 hours. Relative humidity increases again in the late afternoon and evening.

Relative humidity is therefore highest in the early morning and lowest in the mid afternoon. On a seasonal basis, relative humidity is generally highest in late summer (January to May) and lowest in late winter and spring.

Climate classification

According to Schulze (1947), the Lichtenburg study area is in the BSkw class of Köppen. The climate is arid (steppe), cold and dry with a mean annual temperature below 18 °C. Mean temperature of the hottest month exceeds 18 °C and the dry season is during winter. Following the Thornthwaite classification (Schulze 1947, 1958), the study area lies on the border between DB'd to the west and CB'd to the east. DB'd is a semi-arid warm (steppe) climate and CB'd is sub-humid warm. In both climates, moisture is deficient throughout the year. Following the classification of UNESCO-FAO (1963) the climate is accentuated temperate tropical. In other words, there is a dry period of between one and eight months coinciding with the period of shortest day-length, the mean temperature of the coldest month is between 0 °C and 10 °C and the xerothermic index is between 150 and 200.

GEOMORPHOLOGY AND GEOLOGY

Relief

The study area lies between 1460 m (4800 ft) and 1520 m (5000 ft) above sea level (Map 1)[6]. It consists of a large, undulating plain characterised by the absence of any marked topographical features. Gentle rises and shallow hollows throughout and shallow valleys of the Harts River and its tributaries in the south are the most noteworthy topographical features.

Even in this very monotonous landscape a clear relationship between topography and geology is evident. The south-eastern corner is underlain by Archaean granite, which forms dome-shaped hills. This slightly-raised portion is part of the divide between the Harts River to the west and Schoon Spruit to the east. The area occupied by Ventersdorp lava is usually devoid of physiographic features. Volcanic brecchia appears in dome-shaped outcrops and volcanic tuff usually forms a featureless topography.

Dolomite, to the north of Lichtenburg, is usually overlain by a covering of alluvial gravel. Apart from a small escarpment on the road to Zeerust, three kilometres north of Lichtenburg, the area covered by dolomite is very flat, being relieved by occasional chert ridges, shallow depressions, dry watercourses and, more frequently, by sink-holes. Sink-holes are also known as dolines (Lobeck 1939). Some sink-holes are small and have steep sides while

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(6) Maps 1 to 4 are in pocket inside back cover.

others are in the form of long, narrow depressions. Sink-holes have been filled by recent sandy material. The subterranean erosion of dolomite, leading to formation of sink-holes, is described by Harger (1922).

Surface limestone usually builds extensive, flat plains.

Drainage

The south-eastern corner of the area, immediately north of Coligny, is drained by the Taaibos Spruit, which flows into the Schoon Spruit. The south-central area is drained by the Harts River, which rises in a low escarpment immediately north of Lichtenburg and flows towards the south-west. The Harts River does not flow perenially within the area. Usually, the only water in the river bed is in a series of small, shallow, disjunct pools, and artificial dams. North-west of the area drained by the Harts River there is either no surface drainage or run-off is fed to pans with internal drainage. Larger rivers are also lacking in the dolomite area where the water, which is mostly derived from springs, is drained by means of small courses towards the north.

Geological strata

The geology of the area has been described by Von Backström et al. (1953), on which the following account is based. The geological series are mapped on Map 2[6].

1) Archaean granite

Archaean granite occurs south-east of Lichtenburg. Outcrops are rare so that its distribution is mainly deduced from the nature of the terrain and from data obtained from quarries, cuttings and bore-holes. Granite is usually overlain by sandy surface drift.

Granite is white, light grey or pink. The main constituents are feldspar and quartz which, in some cases, form micropegmatite. Microcline and microperthite are present in greater abundance than plagioclase. Mica is also present.

2) Ventersdorp system

Deposits of the Ventersdorp system are found in a belt along the southern edge of the area from the south-western corner to a point south of Lichtenburg and then occur again along the eastern boundary of the area. The system consists mainly of andesitic lava. Intercalated are agglomerate and volcanic conglomerate, pyroclastic sediments or tuff and clastic sediments including boulder conglomerate. As lava occurs at different horizons in the succession, it may be concluded that it was laid down in a number of flows.

The following beds of the System are mapped:- i) quartzite, grit and conglomerate, ii) bedded tuff and tuffy sediments, iii) volcanic brecchia and conglomerate and iv) andesitic lava.

3) Transvaal system

Rocks of the Dolomite series of the Transvaal system are, for the most part, covered by more recent deposits, particularly gravel and surface limestone. Small outcrops occur north and north-east of Lichtenburg, on the boundary of the study area. The Dolomite series consists mainly of blue-grey, massive, dolomitic limestone, with intercalated lenses and layers of chert and shale, the latter being developed more particularly near the base of the Series. The limestone has been strongly chertified and recrystallised.

In many places, dolomite has been weathered chemically. In addition to the general lowering of the level of the dolomite country in this way, localised sub-surface solution has caused numerous, and often large, sink-holes of various depths. Caves, as described by Moon (1972) from a dolomite area 100 km east of Lichtenburg, are not known.

4) Karroo system

Dwyka series tillite and shale of the Karroo system occur over a fairly wide area south and east of Lichtenburg. Owing to fast weathering and the softness of the formation, rocks are seldom exposed at the surface.

Tillite is composed of a soft, clayey, unstratified matrix in which unsorted fragments are spread at random. The fragments are mostly of chert and various quartzites. Examples of glaciated pavements and other distinct signs of glaciation are found.

Shale occurs beneath the tillite in places to form the true base of the Dwyka Series.

5) Tertiary and recent deposits

Economically, these deposits are the most important in the area. They consist of gravel, surface limestone, sand and alluvium.

a) Gravel

Gravel is found mainly overlying Dolomite series rocks in a belt along the northern edge of the area. The deposits, which vary in depth from a few centimetres to over 50 m, are made up of rounded alluvial material with which is mixed angular, eluvial chert.

The alluvial material consists mainly of white, cream-coloured or light grey pebbles of chert and chalcedony although a variety of pebbles derived from other geological systems are also encountered. The eluvial material is composed of angular and irregularly-shaped fragments of chert and concretionary grains of iron, or manganese-iron, derived from weathering of the dolomite floor. Dolomite series rock includes a proportion of very hard, white or grey chert in layers, lenses and veins. As the matrix is dissolved by chemical action, chert remains behind as angular rubble.

From the fossil remains of river beds, known as runs, it has been concluded that the alluvial material was transported from northerly and north-easterly directions by great rivers. The

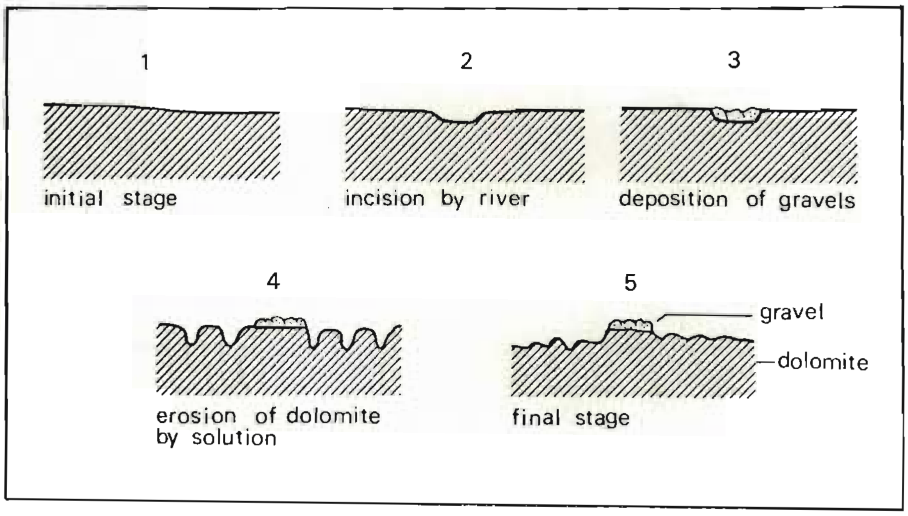

Fig. 2 Development of topography inversion.

original courses, banks and reaches of the ancient river beds may still be determined in places. Some are particularly marked on satellite photographs taken on NASA/ERTS-1 flights.

The fossil river courses are often found protruding above the general level of the surrounding country, instead of being incised into the surface. The phenomenon is known as 'inversion of topography'. The first stages in the inversion is normal incision by the river (see Fig. 2) and the deposition of gravel in the river bed.

<u>INSERT FIG. 2</u>

The alluvial gravel layer then gives a measure of protection from chemical weathering to the underlying dolomite, resulting in a slower lowering of the surface where it is covered by gravel in comparison with surrounding areas. Inversion of topography accounts, in part, for the occurrence of river-bed diamond diggings on small ridges above the general level of the surface.

Stratification of the gravels is distinct in some places and altogether absent in others. The material is either rudely sorted or entirely unsorted and the ratio of rounded to angular fragments varies sharply, even within the same layer. Pebbles and fragments vary in diameter from less than 1,2 cm to more than 1,2 m.

Sink-holes, filled with gravel, are found within the fossil river beds. They were formed before, during, or after the deposition of alluvial material.

b) Surface limestone

Surface limestone covers a large area west of Lichtenburg. It is not generally exposed at the surface, but is covered by a thin, sandy overburden usually from 20 cm to one metre thick. The thickness of the limestone itself is difficult to determine but is known to occur as a thin, hard, crust although it is usually much thicker. Depths between 10 m and 38 m have been recorded. The quality of the limestone varies from some of great purity to some that can be described as calcrete. At the surface, the limestone is usually hard and massive while at greater depths it is softer, granular, friable and slightly stratified.

Vlei-limestone, which differs considerably from surface limestone, occurs locally in the valley of the Harts River. It consists of a mixture of fine, white or light grey chalky material containing varying amounts of crumbly, porous nodules. Lenses of hard, crystalline limestone occur irregularly within it while plant roots, partly or wholly replaced by limestone are locally fairly abundant. The limestone originated through the precipitation of Calcium carbonate from solution in either standing or slowly-moving water. Analyses of water from springs rising from dolomite indicate a mainly dolomitic origin for the Calcium carbonate.

c) Sand

In the area north-west of Lichtenburg the older formations are overlain by red and yellowish Kalahari sand, consisting in the

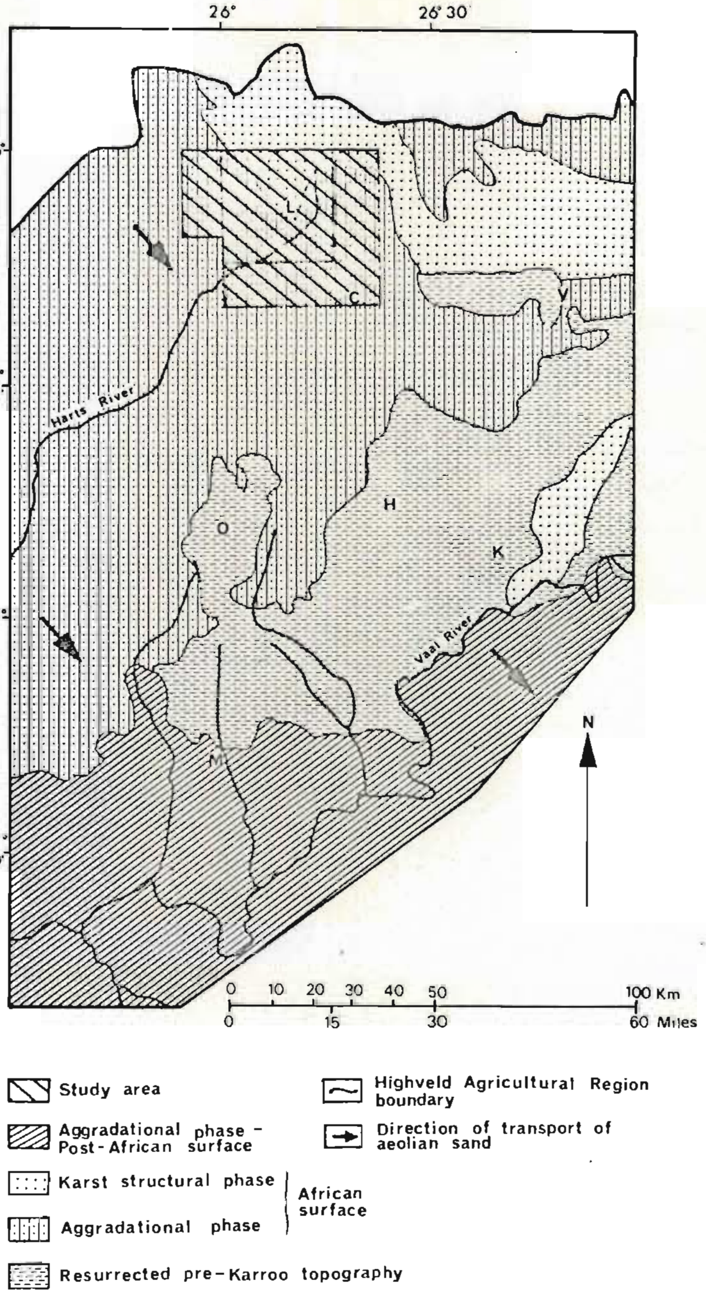

Fig. 3 Erosion surfaces in the Western Transvaal, after Harmse (1967). The study area is hatched. Towns are: L = Lichtenburg, C = Coligny, V = Ventersdorp, H = Hartbeesfontein, K = Klerksdorp, O = Ottosdal, M = Maquassie.

main of slightly rounded grains of quartz, less than one mm in diameter.

South-east of Lichtenburg, coarse-grained sand covers a fairly extensive area. It consists of subangular grains of quartz and felspar with flakes of mica and is mainly derived from underlying Archaean granite.

6) Dyke intrusions

A syenite dyke and occasional diabase dykes are found in the area. Quartz veins are also common throughout.

Erosion surfaces

Erosion surfaces of the Highveld Agricultural Region have been mapped by Harmse (1967). The dolomite, and gravels overlying dolomite, north of Lichtenburg are of the Karst structural phase of the African surface (Fig. 3). Sand overlying the rest of the

INSERT FIG. 3

study area is of the aggradational phase (aeolian sand) of the African surface. Sand was transported from the north-west.

In the succession of erosion surfaces, the African surface is found below the Gondwanaland and Post-Gondwanaland surfaces, which are found on the Drakensberg Mountains and Lesotho Plateau (King 1963). As the African surface is typically flat, the marked absence of relief in the area is understandable.

Economic geology

As the surface mining of diamonds and limestone within the study area influence the natural vegetation these activities are described briefly.

1) Diamonds

Du Toit (1951) made a detailed study of the diamonds and diamondiferous gravels of the area and the following account is based on his findings and those of Draper (1928) and Williams (1930).

The first diamond was discovered in South Africa in 1867 and the famous 'Star of Africa' was uncovered in 1869 (Williams 1930). The first diamond in the Lichtenburg district was discovered during 1921, although diamonds were being mined in the South-western Transvaal before 1914 (Wagner 1914). As diamond discoveries increased at Lichtenburg, more and more fortune hunters arrived and many spectacular 'rushes' were held, culminating in the famous 'charge' on the farm Grasfontein in March 1927 when some 25 000 runners participated. In August 1926, an estimated 56 000 non-Europeans were employed. According to Williams (1930), a population of over 100 000 of every class and colour imaginable was resident on the new diamond fields shortly after their discovery. The presence of this huge population, concentrated in a small area north of Lichtenburg, must have had a marked effect on the vegetation. In addition to direct disturbance by trampling, digging and clearing, the keeping of livestock, gathering of firewood and cultivation of crops probably caused rapid deterioration of vegetation near the diggings.

Up to the end of 1947, the alluvial diamond output of the Lichtenburg district exceeded 7 220 000 carats valued at over £16 006 000 (Du Toit 1951). In 1951, the diggings were still described as the most important of the inland alluvial diggings (Du Toit 1951). Very little activity is evident on the diggings now and only an occasional fortune hunter is encountered.

2) Limestone

The limestone resources of the area are described by Wybergh (1918). Large tracts of surface limestone have been purchased by Anglo Alpha Cement Co. and White's Portland Cement Co., both of which have factories in the area. The thin, sandy overburden is bulldozed away and surface limestone is mined by open-cast methods. Limestone can be mined economically only to a depth of about 14 m. Thus far, no attempt has been made by the Companies to revegetate limestone laid bare on the floors of abandoned mines. Limestone dust, blown from this source, is a problem as the surface is not protected from wind erosion. Natural vegetation is not able to invade the bare limestone surface adequately without considerable assistance.

TABLE 1 Comparison of soil series names applied to soils of the 2626AA quarter degree square.

Names used by Van der Bank (1968)	Names presently accepted by the Soils and Irrigation Research Institute (after Verster).
Lichtenburg series	Lichtenburg series
Rietdraai series	Lichtenburg series
Hendriksdal series	Shorrocks series
Mangano series	Mangano series
Rooigrond series	Shorrocks or Mangano series
Sinkgat series	Mangano series
Rietgat series	Soetmelksvlei series
Greefslaagte series	Soetmelksvlei series
Ventersdorp series	Soetmelksvlei series
Soetmelksvlei series	Soetmelksvlei series
Vlakfontein series	Soetmelksvlei series
Hartsrivier series	Rensburg series
Manana series	Bonheim series
Klippan series	Willemsdal or Sterkspruit series
Kalkbult series	Shorrocks series
Dudfield series	Soetmelksvlei series
Kalkbank series	Muden series (fine sandy type)
Brakpan series	Arcadia or Muden series

SOILS

Introduction

Soils of the 2626AA quarter degree square have been mapped by Van der Bank (1968) and the reader is referred to that publication for a detailed description of soil genesis, structure and composition. Soils of that part of the study area outside the 2626AA quarter degree square have **not** been mapped. Van der Bank describes in detail a total of 21 soil profiles of the 18 soil series recognised. His map of 17 soil series, four soil complexes and three land classes has been simplified in collaboration with E. Verster[7] to nine soil series, four complexes and three other classes to conform with present soil nomenclatural concepts of the Soils and Irrigation Research Institute. The simplified map is given as Map 3[6]. A comparison of the names applied to soil series in the Lichtenburg area by Van der Bank (1968) and Verster is given in Table 1.

INSERT TABLE 1

Shorrocks, Mangano and Lichtenburg Series

Shorrocks series soils occur in small patches north-west of

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(7) Address: Dr E. Verster, Soils and Irrigation Research Institute, Belvedere St., Pretoria.

Lichtenburg. Mangano series occur very locally within the Dolomite region north of Lichtenburg while Lichtenburg series cover relatively small areas near the Harts River in the south-eastern corner of the study area.

Shorrocks, Mangano and Lichtenburg Series are well-drained soils. They are characterised by good internal drainage and weak structure. They have high, fine sand and low clay content, prominent red colours and an absence of mottling. Horizons that impede drainage are absent. Kaolinite is the principal clay mineral and the exchange capacity varies between two and eight milli-equivalents percent. Calcium and magnesium are the dominant exchange cations throughout the profile. In the surface horizons, exchange calcium is dominant, but in the underlying horizons magnesium increases rapidly and may even exceed calcium.

Soetmelksvlei Series

Soetmelksvlei is the non-lithosol series covering the largest area in the quarter degree study area. It occurs throughout the area not underlain by dolomite.

Restricted drainage is a characteristic of Soetmelksvlei soils. With increasing depth the clay content increases and the structure becomes weak medium blocky. Red and yellow mottles associated with uncemented iron concretions are distinctive features of the lower horizons. Principal clay minerals are kaolinite and illite. Montmorillonite tends to increase in the lower horizons. Exchange capacities vary between four and eight milli-equivalents percent. Calcium and magnesium are the dominant cations. Magnesium increases with depth but seldom exceeds calcium.

Rensburg, Bonheim and Willemsdal or Sterkspruit Series

The Rensburg, Bonheim and Willemsdal or Sterkspruit series are poorly-drained soils. Poor permeability, high clay content, high exchange capacity and strong blocky or prismatic structure are the salient features of these Series.

The occurrence of these soils, either collectively or singly, is limited in extent. Rensburg series occurs in the bed of the Harts River while Bonheim series soils are restricted to slopes of the Harts River valley, where the river leaves the dolomite substrate. Willemsdal or Sterkspruit series occur in small patches north and north-west of Lichtenburg. They are usually underlain by dolomite.

Muden and Muden or Arcadia Series

The feature common to Muden and Muden or Arcadia series soils is the underlying surface limestone formation encountered at shallow depths. Where the limestone is buried deeper the soil is usually Soetmelksvlei. The parent materials are either aeolian sand, drift materials, or both.

These soils cover areas of moderate size, usually in complexes, to the west of Lichtenburg.

Differences in emphasis between pedologist and plant ecologist

The soil survey by Van der Bank (1968) clearly illustrates the differences in emphasis placed by pedologists and plant ecologists in the same area. He describes, in detail, soils which are under very heavy cultivation while the dolomite lithosol receives scant mention. On the other hand, the natural vegetation of the ploughed area is solely of historical importance while the vegetation of the unploughed areas (the lithosols) has economic and academic value. These differences in emphasis, unfortunately, hinder correlation between soil and vegetation surveys.

In describing the vegetation of the area, Van der Bank mentions the Veld Types described by Acocks (1953) and then records that the natural vegetation has been largely destroyed by ploughing and it is only in the corners of fields that vegetation in fairly good condition may be found. The small grazing paddocks which remain on the ploughable areas are usually so overgrazed and the vegetation is so damaged that the original species composition has undoubtedly changed, according to Van der Bank. As far as the dolomite area is concerned, he merely mentions that in addition to grasses a few tree species occur.

The difference in outlook between Van der Bank and the writer is most marked; in the following chapters it is the vegetation of the dolomite areas which receives most attention.

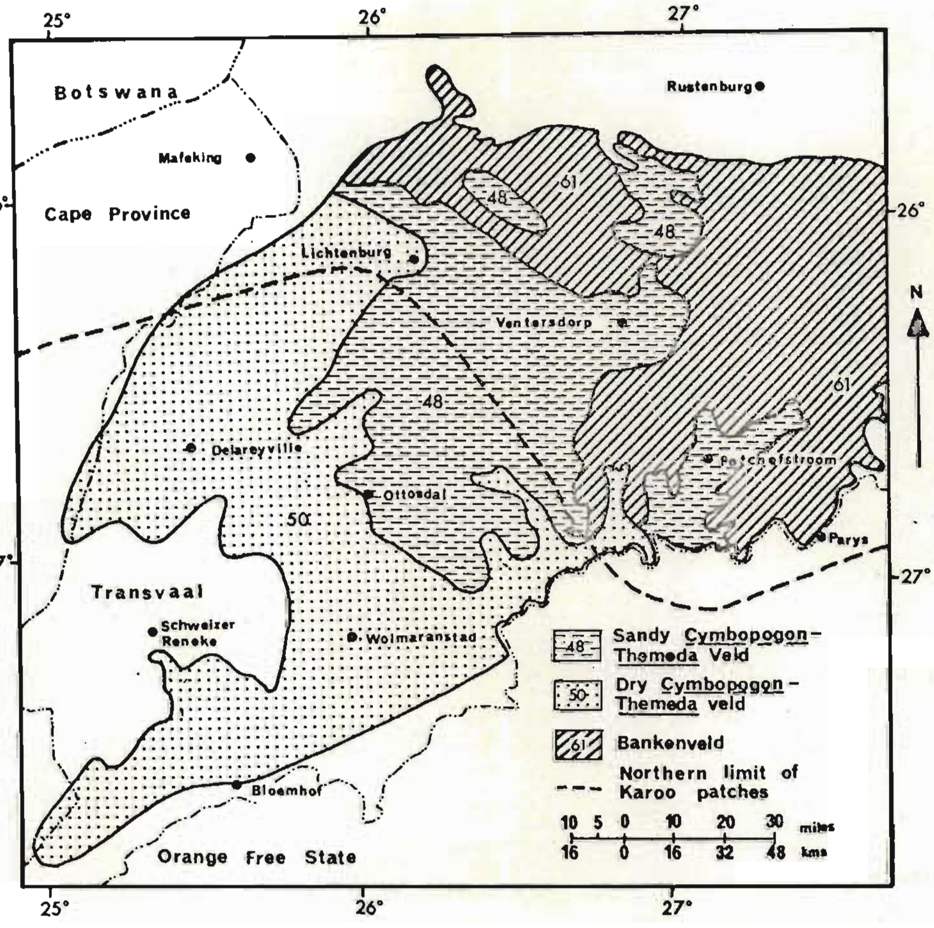

Fig. 4 Distribution of Veld Types (Acocks 1953) in the South-western Transvaal.

VEGETATION

This account is based on the description of Acocks (1953)[8]. The distribution of Veld Types (Acocks 1953) in the South-western Transvaal is shown in Fig. 4. Most of the study area west of

INSERT FIG. 4

Lichtenburg is covered by Dry Cymbopogon-Themeda Veld (Veld Type 50). An area of Sandy Cymbopogon-Themeda Veld (48) extends north of Lichtenburg towards Mafeking and covers the rest of the 2626AA quarter degree square. Further north, outside the study area, Bankenveld (61) occurs.

In the South-western Transvaal, Dry Cymbopogon-Themeda Veld occurs in an arc from Lichtenburg to south-west of Delareyville and then south to Wolmaransstad. This arc, comprising the northern variation of the Veld Type, is found on sandy soils. The dominant species is *Themeda triandra*. *Cymbopogon plurinodis* is the tallest grass, but is usually not common. This Veld Type lies between altitudes of 1280 m (4200 ft) and 1370 m (4500 ft) on flat, sandy country with a summer rainfall of 430 to 580 mm (17-23 in) per

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(8) Species names used by Acocks have been brought up to date where possible.

TABLE 2 Species of general occurrence, according to Acocks, in Dry Cymbopogon-Themeda Veld (50), Sandy Cymbopogon-Themeda Veld (48) and Bankenveld (61) with relative abundances of over 1000 (relative abundance values are given in thousands).

Species	Veld Type 50	48	61	
Setaria flabellata	142	121	109	Common to all three Veld Types
Heteropogon contortus	7	27	76	
Eragrostis chloromelas	5	20	36	
Elionurus argenteus	11	16	35	
Themeda triandra	165	39	30	
Cymbopogon plurinodis	37	13	13	
Eragrostis racemosa		20	137	Common to Bankenveld and one other Type
Brachiaria serrata		13	15	
Diheteropogon amplectens		1	14	
Triraphis andropogonoides	2		2	
Eragrostis lehmanniana	26			Found in Dry Cymbopogon-Themeda Veld
Anthospermum rigidum	8			
Eragrostis superba	6			
Eustachys mutica	5			
Anthephora pubescens	5			
Eragrostis obtusa		2		Found in Sandy Cymbopogon-Themeda Veld
Vernonia oligocephala		2		
Eragrostis gummiflua		2		
Eragrostis capensis		1		
Digitaria tricholaenoides			120	Found in Bankenveld
Trachypogon spicatus			15	
Tristachya rehmannii			5	
Justicia anagaloides			5	
Bulbostylis burchellii			5	
Schizachyrium sanguineum			4	
Cassia mimosoides			3	
Senecio venosus			3	
Acalypha angustata			3	
Diplachne biflora			2	
Helichrysum caespititium			2	
Trichoneura grandiglumis			1	

annum and with frosty winters. Species of general occurrence are given in Table 2.

INSERT TABLE 2

Species of less general occurrence include: Cynodon dactylon, Digitaria argyrograpta, Digitaria eriantha, Panicum coloratum and Stipagrostis uniplumis. There were 140 species in the Relative Abundance Table (Acocks 1953).

In the South-western Transvaal, Sandy Cymbopogon-Themeda Veld occurs in the rough square bounded by Lichtenburg, Ventersdorp, Klerksdorp and Ottosdal, to the immediate east of the arc of Dry Cymbopogon-Themeda Veld. The square comprises the northern variation of the Veld Type where the altitude ranges from 1310 m (4300 ft) to 1520 m (5000 ft) and summer rainfall is from 510 to 690 mm (20-27 in). Winters are frosty. Species of general occurrence are listed in Table 2. Species of less general occurrence include Cynodon dactylon, Cynodon incompletus, Digitaria argyrograpta and Helichrysum rugulosum. According to Acocks, this Veld Type merges into the western variation of Bankenveld and needs more study. Dry Cymbopogon-Themeda Veld usually occurs at a slightly lower elevation than Sandy Cymbopogon-Themeda Veld and usually receives slightly less rain.

Sandy Cymbopogon-Themeda Veld and Dry Cymbopogon-Themeda Veld are both Pure Grassveld Types while Bankenveld is a False Grassveld type. Bankenveld occurs in a belt from east of Ventersdorp, to Klerksdorp and Parys. The western variation occurs near Lichtenburg. It is found on sandy plains and low, rocky ridges, ranging in altitude from 1370 m (4500 ft) to 1680 m (5500 ft) and receives 560 to 690 mm (22-27 in) rain, mostly in summer. It is a rather sparse, sour, strongly tufted vegetation and, in the nature of its grasses, is clearly transitional from Sandy Cymbopogon-Themeda Veld to Sour Bushveld (Veld Type 20), which occurs north of the study area, according to Acocks. The climax was possibly an open savanna with Acacia caffra. Species of general occurrence are given in Table 2. Species of less general occurrence include:- Anthospermum rigidum, Digitaria pentzii var. stolonifera, Digitaria monodactyla, Eustachys mutica, Kohautia amatymbica and Pygmaeothamnus zeyheri. Two hundred and three species occurred in the Relative Abundance Table.

Six species occur commonly in all three Veld Types (Table 2) and four occur in Bankenveld and one other Type when species with relative abundances (as defined by Acocks 1953) of over 1000 are taken as being 'common'. Twelve species occur commonly only in Bankenveld while four and five occur commonly only in Sandy Cymbopogon-Themeda Veld and Dry Cymbopogon-Themeda Veld, respectively. Although relative abundance values were not designed for this application, they give an overall view of the distributions of common species within the three Veld Types concerned.

Tentative boundaries to Veld Types drawn by Acocks (1953) for the South-western Transvaal (Fig. 4) may be re-drawn after more intensive study. Limits of Bankenveld near Potchefstroom and Ventersdorp, east of the study area, have been accurately mapped by Grunow (1959). Photographs from NASA/ERTS-1 flights will greatly aid the further mapping of vegetation in this area at reconnaissance scales. Bankenveld is actually found as far south as Lichtenburg, as far west as a line from Lichtenburg to Mafeking and as far east as a line from Lichtenburg to Rustenburg although this is not apparent from Acocks' map. Whether the rest of the area was Dry *Cymbopogon-Themeda* Veld or Sandy *Cymbopogon-Themeda* Veld is of academic importance only as the natural vegetation has been replaced by extensive cultivation.

LAND-USE

Broad land-use is closely tied to geology, soils and vegetation. The areas with deep, well-drained soils overlying all geological systems except dolomite (Dry *Cymbopogon-Themeda* Veld and Sandy *Cymbopogon-Themeda* Veld) are extensively ploughed. Van der Bank (1968) comments that, in practice, all soils which are ploughable have already been ploughed. The principal crop is maize and limited quantities of sunflowers, grain sorghum, groundnuts and cattle fodder are grown. It is estimated by Van der Bank (1968) that the average yield of the crop is about 15 bags per morgen (1170 kg/ha) although some farmers reap 20 or more bags per morgen (1550 or more kg/ha). According to J.O. Grunow[9], 12 to 15 bags per morgen are required to cover costs.

Cattle ranching is the chief occupation of farmers on the dolomitic lithosols (Bankenveld) north of Lichtenburg. Occasional

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(9) Address: Prof. J.O. Grunow, Dept. of Pasture Science, University of Pretoria, Pretoria.

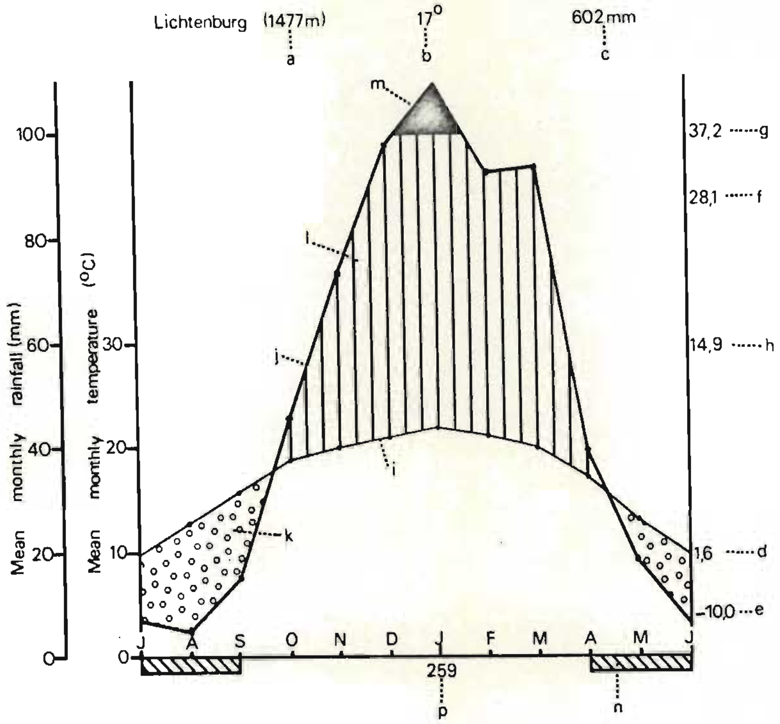

Fig. 5 Climate diagram for Lichtenburg (a = altitude, b = mean annual temperature, c = mean annual precipitation, d = mean daily minimum temperature of coldest month, e = absolute minimum temperature, f = mean daily maximum temperature of hottest month, g = absolute maximum temperature, h = mean range of temperature, i = curve of mean monthly temperature, j = curve of mean monthly precipitation, k = dry season, l = wet season, m = mean monthly precipitation over 100 mm, n = months with absolute daily minimum temperature below 0°C, p = mean duration of frost-free period in days).

sink-holes in the area, which have become filled with aeolian sand, are invariably cultivated for cash crops like maize. Some irrigation, using the good supplies of water from boreholes, is undertaken.

An alarming activity is the open-cast mining of surface limestone in the area by two cement Companies. Large tracts have been acquired and are being systematically laid desolate. Unaided colonisation of denuded areas by plants is very slow and a means of accelerating colonisation is needed as wind-blown dust from the denuded areas is a problem.

SUMMARY OF ENVIRONMENTAL FEATURES

Climate

The climate of the Lichtenburg study area is summarised in the diagram (modified after Walter & Leith 1960) given in Fig. 5.

INSERT FIG. 5

Aspects of weather and climate over Southern Africa are summarised by Jackson (1951) and Jackson & Tyson (1971). They detail the influence of the position of the subcontinent in relation to pressure and wind systems of the Southern Hemisphere, off-shore ocean currents and other factors, on rainfall distribution. Types of weather and climatic elements including radiation, sunshine, precipitation and temperature over Southern Africa are also described.

In the following summary, use is made of the description of climate given by Schulze (1965) for region H (the Highveld) in his description of the climatic regions of South Africa. The average daily maximum temperature is about 28 °C in January and 18 °C in July but in extreme cases temperatures may rise to 37 °C and 25 °C, respectively. Average daily minima range from about 15 °C in January to 2 °C in July, whereas extremes may drop to 6 °C and -10 °C, respectively. The period during which frost is likely to occur lasts, on average, for 106 days from May to September, during which period frost occurs on about 26 days. Sunshine duration in summer is about 60 percent and in winter 80 percent of the possible.

Mean annual precipitation is about 600 mm. Rainfall is almost exclusively due to showers and thunderstorms. Winter months are normally dry and about 85 percent of the annual precipitation falls during the summer months from October to March. A small rainfall peak occurs in January. Heavy falls of 125 mm to 150 mm are occasionally recorded in a few hours. The average annual number of thunderstorms is about 75. These storms are often violent with severe lightning and strong, but short-lived, gusty, south-westerly winds and are sometimes accompanied by hail. The area has a high hail frequency with an average of four to seven occurrences annually.

Other environmental features

When relief, geology, geomorphology, soils, vegetation and land-use are considered, two very different Land Systems (Dowling 1968, Mabbutt 1968) or bioclimatic[(3)] regions (Phillips 1973) may be recognised in the study area. According to Dowling and Mabbutt, the land of a region is conceived as a series of Land Systems, each of which contains typical land facets, which have similar features wherever they occur and which can be readily identified on aerial photographs. In the following summary of environmental features each Land System is treated separately.

One Land System, named Bankenveld, is underlain by dolomite, variously covered by alluvial gravels on the Karst structural phase of the African erosion surface, and with lithosolic soils. The Veld Type is Bankenveld and cattle ranching is the chief land-use.

The second Land System, named CT Grassland, is underlain by granite, Ventersdorp lavas, Dwyka tillite and surface limestone on the aggradational phase (aeolian sand) of the African erosion surface. Soils of Shorrocks, Mangano and Lichtenburg series are generally sandy and well-drained. The natural vegetation was Dry Cymbopogon-Themeda Veld or Sandy Cymbopogon-Themeda Veld but most of it has been destroyed for the cultivation of maize, the chief land-use.

CHAPTER 3

C L A S S I F I C A T I O N O F T H E V E G E T A T I O N B Y A S S O C I A T I O N A N A L Y S I S

INTRODUCTION

In this Chapter, which gives a quantitative description of the vegetation of the study area, the sampling strategy and method of classification are first described. Classification results and descriptions of each plant community are given in the next, and largest, section of the Chapter. The results and sampling strategy are briefly discussed in the last section.

PROCEDURE

Sampling strategy

A major consideration in designing the vegetation sampling strategy was compatibility with other component projects of the ecological survey of the Highveld Agricultural Region. A common sampling strategy will make possible meaningful comparison between surveys and their results and enhance possibilities for integration and extrapolation between areas surveyed by different officers. As J.C. Scheepers(1), who is responsible for surveying the eastern section of the Region, had started field sampling before the study reported here was initiated, his general strategy was adopted.

1) Sample placement and size

Initially, the 2626AA **quarter** degree square (bounded by 26° 00' and 26° 15' east longitude and 26° 00' and 26° 15' south latitude) was taken as the study area. All lands under cultivation, or showing signs of past cultivation, as well as the town of Lichtenburg were excluded from the area to be sampled as indicated by hatching on 1:36 000-scale aerial photographs. The remaining area was stratified into Bankenveld and CT Grassland Land Systems. Within each Land System, unploughed areas were stratified into physiognomic-physiographic units determined on aerial photographs. Although relatively few units could be recognised as the area is without marked features, such physiographic features as the Harts River could be distinguished from the surrounding plains. Within the Bankenveld Land System, no physiognomic subdivisions were possible but sink-holes and narrow strips of Willemsdal or Sterkspruit and Shorrocks or Mangano soils were delimited.

In addition to lands under cultivation and the town of Lichtenburg, no samples were placed in or near the bed of the Harts River. A number of considerations lead to this decision.

Firstly, the area covers a small proportion of the whole study area and, secondly, the floristic and habitat differences between the river bed and higher-lying areas were so obvious that automatic methods were considered unnecessary for elucidating the differences. The third reason was that although very little of the river-bed had been ploughed, the vegetation had been severely overgrazed and trampled and some re-seeding had been carried out, all of which had modified the vegetation to such an extent that standard samples could not have been considered reliable abstractions of the natural vegetation that existed there previously.

Within each physiognomic-physiographic unit, sample positions were marked on aerial photographs at random, using pairs of random co-ordinates. The number of samples in each unit was proportional to the area covered by the unit on the photographs with small units being given slightly more samples than large units in proportion to the area they covered. It was attempted to place at least five samples in each unit. A total of 250 sample positions were marked on photographs as it was considered that between 200 and 250 samples could be taken during the one summer allocated for fieldwork. In certain parts of the study area, extensive cultivation resulted in only small, fragmented areas being suitable for sampling. Even by clustering samples closely, it was found impossible to obtain a representative sample of the CT Grassland Land System within the quarter degree square. The study area was, therefore, enlarged westwards to 25° 54' east, southwards to 26° 20' south and eastwards to 26° 22' east, so that enough samples of vegetation could be obtained.

The sample size of 16 m^2, chosen during pilot studies for the Highveld Survey Project, was retained for uniformity. Pilot studies had shown that a sample area of 16 m^2 was both the smallest adequate sample for grassland vegetation of this kind and the largest area that could be sampled in an economically-justifiable time (J.C. Scheepers[1]: pers. comm.).

For technique studies during the present survey, however, it was decided to record species presence in such a way that samples of other sizes would be obtained as a by-product. The basic, 4 by 4 m sample, constructed of fine chain stretched between stakes, was divided into four triangles by chains connecting diagonally-opposite corners of the square. Each triangle covered 4 m^2. Samples of 4, 8, 12 and 16 m^2 were thus available by successive addition of triangles. Species present in a belt, estimated as being two metres wide, round the perimeter of the sample were also recorded, principally to aid re-allocation of samples mis-classified by association analysis owing to the chance absence of the positive dividing species. A sample of approximately 64 m^2 was obtained thus. For technique studies, areas of 4, 8, 16 and 64 m^2 were used.

Each sample point, marked by a pin-prick on an aerial photograph before going into the field, was found as precisely as possible by study of the photograph at the site. Once the position had been found, and if it had not been ploughed since aerial photography, a metal stake was thrown over the recorder's shoulder. The point where the marked end of the stake came to rest became the north-west corner of the sample, which was aligned north-south and east-west by magnetic compass sightings. The random element introduced by throwing the stake and the use of the same sample alignment each time excluded intentional and subconscious selection for or against a particular stand of vegetation.

A metal stake (fencing dropper) was hammered into the ground to mark the north-west corner of the quadrat permanently for accurate relocation of the sample if necessary.

2) Habitat data gathered

A limited amount of habitat information was recorded at each sample site. Physical factors recorded for each site included geology, geomorphology, aspect, angle of slope and exposure. Soil type (Van der Bank 1968) and depth were recorded and then for each horizon, soil pH (measured by colorimetry[10]), soil reaction to dilute hydrochloric acid (HCl), moist soil colour (Munsell) and soil texture were noted. Biotic influence was noted by animal type and by degree on a four-point scale from absent to very intense.

3) Vegetation data gathered

Total basal cover and height and basal cover of each constituent stratum were estimated for the 16 m^2 sample.

The presence of all permanently-recognisable plant species was recorded. The order in which each species was encountered was

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(10) Approximately five g soil in five ml distilled water with one g Barium sulphate as clearing agent.

noted, as were additional species found with each increase in sample size from 4 m^2 to 64 m^2. Cover-abundance on the Braun-Blanquet scale (Werger 1973) was also noted for each species.

Association analysis

An objective method for classifying the vegetation of the study area was required. At the time of sampling, the only method known to be suitable was the hierarchical technique of the Southampton-Canberra school (Williams & Lance 1958, Williams & Lambert 1959, 1960, 1961a, Lambert & Williams 1962, and others). The original technique, association analysis (Williams & Lambert 1959), has been used with varying degrees of success in a number of vegetation types in South Africa, including Van der Walt (1962) in grassland, mountain scrub and karroo vegetation, Grunow (1965a, b and 1967) in bushveld, Roberts (1966) in grassland, Downing (1966) in vlei vegetation, Miller (1966), Miller & Booysen (1968) and Scheepers (1969) in grassland, Taylor (1969) and Boucher (1972) in fynbos, Downing (1972) in savanna and woodland vegetation and Coetzee (1972) in Bankenveld. Although more advanced analyses had been successfully carried out (for example: Grunow & Lance 1969), the computer programs were not available in South Africa.

It was decided, on pragmatic grounds and in spite of possible shortcomings and limitations in the technique, to use association analysis for classifying the vegetation and then to carry out other, more sophisticated, analyses as part of a later comparative technique study.

The monothetic-divisive technique of association analysis, used for classification, is so well known as not to require detailed description. Briefly, quadrats to be classified are hierarchically divided on the basis of the presence or absence within each quadrat of the species with the highest association (X^2 in one or other form[11]) with every other species. Division by this strategy has been found to remove most heterogeneity from the parent population of quadrats, resulting in groups with a higher degree of homogeneity than any other grouping.

An analysis was carried out on the 220 quadrats (16 m^2) of the study area and then another was carried out on the 110-quadrat subset of Bankenveld Land System quadrats. The former, known below as the Total analysis, was done to obtain an overall classification of the vegetation of the area and, in particular, to enable definition of the main vegetation types. The second analysis, known as the Bankenveld analysis, was to obtain in-depth information about Bankenveld, the area whose natural and semi-natural vegetation was of most importance. The Bankenveld analysis was necessary as the Total analysis did not separate Bankenveld from CT Grassland Land Systems clearly enough. In both analyses, the division parameter used was $\sum(X^2/N)^{\frac{1}{2}}$. Subdivision was terminated when the highest single X^2 (with Yates' correction) failed to exceed

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(11) X^2 is used for chi-square throughout this account.

3,84 (p = 0,05), or less than eight quadrats remained in the group[12]. For each analysis, species occurring in fewer than six quadrats were masked as it was presumed that those species were rare enough not to have Indicator value. Their exclusion greatly increased the speed of computation. The influences of various kinds of data reduction are discussed in a later Chapter.

For each analysis, straight lines were drawn across the hierarchies at fairly low highest single X^2 levels and groups existing at those levels were numbered from left to right. From the chosen level, groups were interpreted downwards to the final groups of the analysis and upwards to the first division.

It was required that defined groups be given names and not be known only by numbers, or letters, as done by Grunow (1965a) and many others. The suffix 'Bankenveld' was used for all groups of the Bankenveld Land System and 'Grassland', 'Woodland' and 'Savanna' suffixes were used for association analysis groups of the CT Grassland Land System. One or two species were chosen for inclusion in the name. Where possible, positive dividing species from the association analysis were used but species with significant Indicator values or high cover-abundance ratings (see later) were also used. In order to create unique names, it was sometimes necessary to overlook a species which appeared suitable as it was even more appropriate for another group. Derivations of names are discussed either in the

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(12) The neutral term 'group' is preferred to 'association', which has a specific meaning in the Braun-Blanquet sense (Werger 1973), while other neutral terms like 'community' could have been used.

group descriptions or in the discussion of similarities between groups. For economy of reference in the text, groups are usually referred to by numbers and letters, instead of by their full names.

Indicator value and other aids for group interpretation

Program CFREQ, written by the author, was used to aid interpretation of groups at all hierarchical levels. The program lists species occurring in more than 19 percent of the quadrats of a given collection of quadrats together with their absolute and percentage presence within the group. As Cain & Castro (1959) define constancy as, "a relative expression of the presence and absence of plants of a species in different stands of a community type, based on equal-area samples" (p. 288), constancy might seem to be a term preferable to presence, which they define as, "the degree to which a species is represented in a series of stands of a community type" (p. 295). To avoid confusion with the so-called Roman or constancy table of the Braun-Blanquet school (Werger 1973), presence and presence percentage are used throughout this account even though equal-area samples were used and constancy is therefore possibly more correct.

Indicator value (Goodall 1953b) for each species is also calculated by CFREQ. Indicator value, according to Goodall, is used to express the presence of a species in a particular group against its presence in all other groups. Where a species has lower presence in a group than in all the other groups together, Indicator value will be negative; otherwise it is positive.

Consider the following 2 by 2 contingency table where presence and absence of a species in Group A and in all other groups are given:-

	Group A	all other Groups	
species x present	a	b	a + b
species x absent	c	d	c + d
	a + c	b + d	N

Indicator value (IV) is given by:-

$$IV = \frac{(a - \frac{1}{2})(b + d)}{(b + \frac{1}{2})(a + c)} - 1$$

where Yates' correction for continuity has been applied. Where b is greater than a, Indicator value is calculated as:-

$$IV = \frac{(b - \frac{1}{2})(a + c)}{(a + \frac{1}{2})(b + d)} - 1$$

and is given a negative sign. The significance of Indicator values may be calculated by X^2 (either with Yates' correction or by Fisher's exact test, whichever is appropriate). In the following account, species with positive, significant (p = 0,05) Indicator values are marked IVS, while species with negative, significant Indicator values are marked -IVS.

The lists of species with negative Indicator values are not complete, however, as only species present in more than 19 percent of the quadrats of each group are listed by CFREQ. Many more species may have significant, negative Indicator values as such values are more common among species with low presence in a group.

Re-allocation

Inspection of final groups suggested that on the bases of their habitat data being markedly dissimilar from those of other quadrats of the group, certain quadrats were misclassified. By reference to species listed from the area surrounding each 4 by 4 m quadrat they were re-allocated to other groups on the basis of the dividing species of the hierarchy. Some quadrats, which, from inspection, appeared misclassified but which could not be satisfactorily re-allocated by the above method were left in their original groups and are discussed with those groups, as exceptions.

Mapping of vegetation

A vegetation map of the study area was drawn at a scale of 1:50 000. Extensive use was made of aerial photographs to identify groups obtained by means of the association analysis. The physiognomic-physiographic stratification, completed prior to sampling, was used and detail was transferred from photographs to the base map by means of a radial-line plotter. As certain association analysis groups could not be distinguished separately on photographs, they were mapped together. Where identification on photographs was not certain, a field check was made before final mapping.

Vegetation boundaries were drawn to include as many quadrats

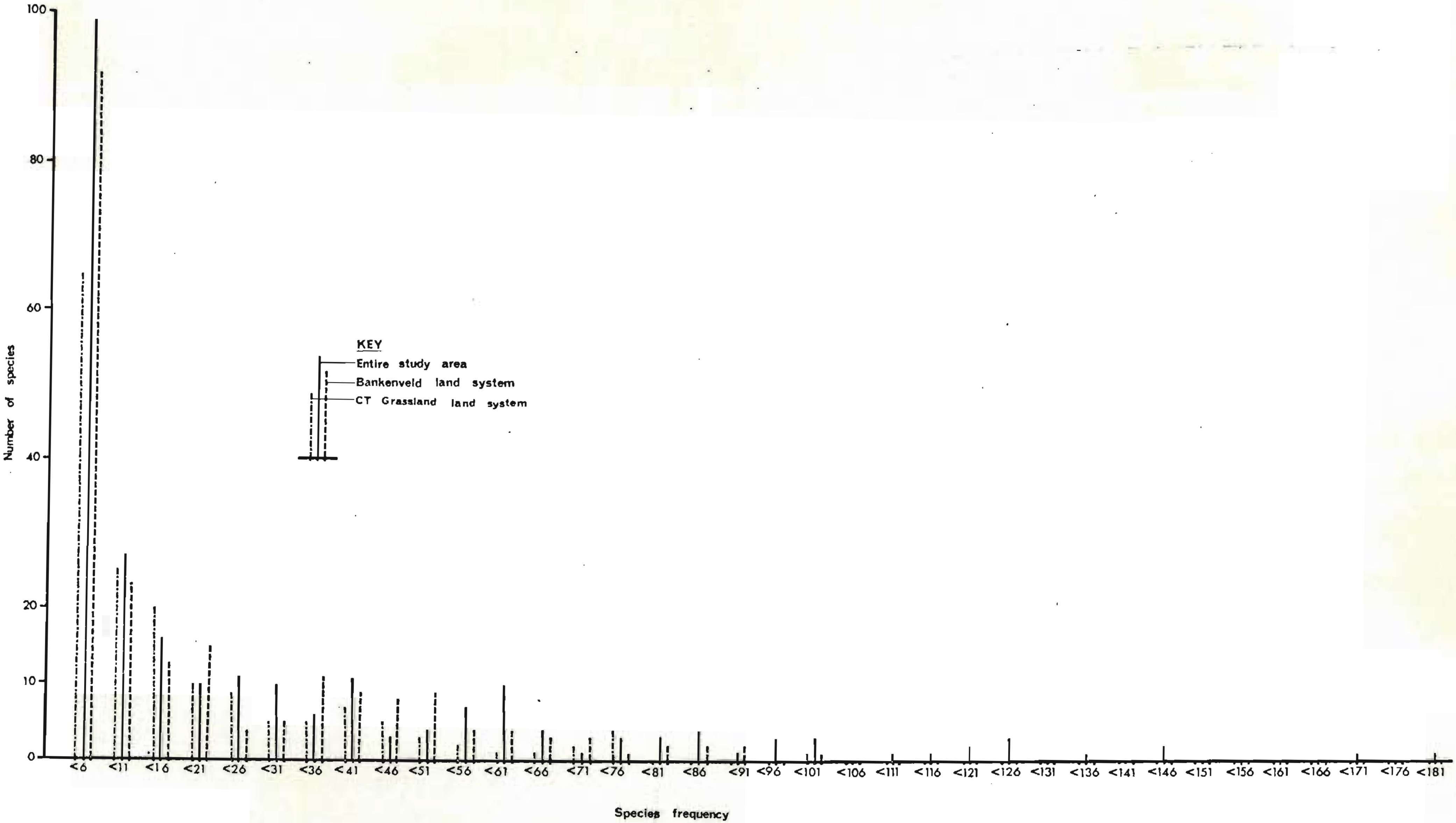

Fig. 6 Number of species present in each species frequency class over entire study area, within Bankenveld and within CT Grassland Land Systems.

of a group, as possible, within the boundaries of the group to which they belonged. For some quadrats this was, however, not possible.

RESULTS

Summary statistics of data

A total of 220 quadrats were placed within the study area. Between the 2nd March and 10th April 1970, 110 sample plots were taken in the Bankenveld Land System and between 27th April and 27th May 1970, 110 quadrats were laid out in the CT Grassland Land System. An average of nearly seven samples were taken on each working day in CT Grassland and the average in Bankenveld was over six each day. Locations of the 220 sample sites are indicated on Map 4(6).

The following statistics refer to the 16 m^2 quadrats unless otherwise indicated. The number of species encountered in all the quadrats was 247. Within Bankenveld 211 species were encountered, only 36 fewer than in all the quadrats, whereas only 165 species were found in CT Grassland quadrats. Proportions of common and uncommon species are summarised in Fig. 6. Shapes of all three

INSERT FIG. 6

graphs indicate that many species are uncommon (have low overall presence) and that a few species are very common (have high overall presences). Within the entire area nearly 100 species occurred in fewer than six quadrats. Of these, 35 occurred in only one quadrat and 26 in only two quadrats. As nearly 40 percent of the species were uncommon (occurring in five or fewer quadrats), it was decided to mask uncommon species from the association analyses. Within Bankenveld, 92 species occurred in fewer than six quadrats, 42 species occurred in only one quadrat and 24 were found in only two quadrats.

The commonest species in Bankenveld were Aristida congesta, Justicia anagaloides and Themeda triandra occurring in 97, 87 and 86 of the 110 quadrats, respectively. Over the entire study area (220 quadrats), Themeda triandra was the species occurring most frequently (in 184 quadrats). Other commonly-occurring species were Aristida congesta (171 quadrats), Elionurus argenteus (150 quadrats), Anthospermum rigidum (149 quadrats) and Justicia anagaloides (136 quadrats).

A Bankenveld quadrat contained the largest number of species (54). In CT Grassland, the highest number of species in a quadrat was 36. In Bankenveld, the lowest number of species in a 16 m^2 quadrat was 18, in a 64 m^2 quadrat it was 19 and in CT Grassland (16 m^2) it was 11. The average number of species in a Bankenveld quadrat was 36,5 (standard deviation (SD) = 7,5) and in CT Grassland the average was 24,3 (SD = 5,5). The overall average was 30,4 (SD = 9,0).

In summary, about 30 species were recorded in each of the 220 quadrats, a larger number of species being found in Bankenveld quadrats than in CT Grassland quadrats. About 40 percent of the species could be considered uncommon and only four species occurred

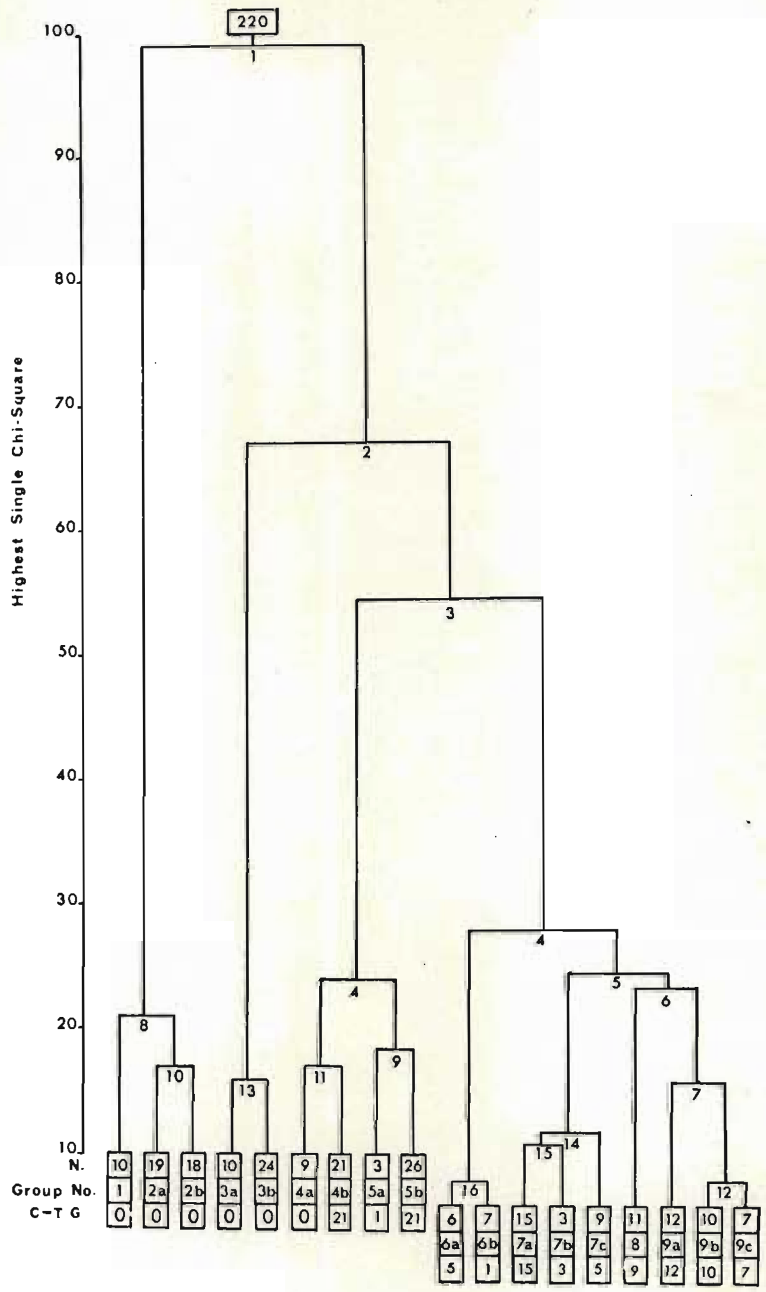

Fig. 7 Association analysis hierarchy of Lichtenburg study area. N. = total number of quadrats in each group and C-TG is number of CT Grassland Land System quadrats in group. Dividing species are: 1 = <u>Schizachyrium sanguineum</u>, 2 = <u>Kohautia omahekensis</u>, 3 = <u>Brachiaria serrata</u>, 4 = <u>Stipagrostis uniplumis</u>, 5 = <u>Crabbea angustifolia</u>, 6 = <u>Heteropogon contortus</u>, 7 = <u>Triraphis andropogonoides</u>, 8 = <u>Eustachys mutica</u>, 9 = <u>Bulbostylis burchellii</u>, 10 = <u>Loudetia simplex</u>, 11 = <u>Indigofera daleoides</u>, 12 = <u>Barleria macrostegia</u>, 13 = <u>Eragrostis lehmanniana</u>, 14 = <u>Hermannia depressa</u>, 15 = <u>Blepharis integrifolia</u>, 16 = <u>Vernonia oligocephala</u>.

in over 65 percent of all quadrats.

Total association analysis

1) Description of hierarchy

The association analysis hierarchy classifying all 220 quadrats is given in Fig. 7. The quadrats are divided into four major groups.

INSERT FIG. 7

These four groups are very distinct, being maintained from a level of H.S.$X^2 > 54,0$(13) to H.S.$X^2 < 28,5$ in the case of the third and fourth groups and more than double that amount in the case of the first group. At a level of H.S.$X^2 = 20,0$ there are nine groups and at a level of H.S.$X^2 = 15,0$ there are 14 groups. At the 14-group level the mean number of quadrats per group is 15,7. Inspection of the results showed that certain subgroups of the fourth major group could be profitably subdivided to a lower level than H.S.$X^2 = 15,0$. Thus, divisions above H.S.$X^2 = 7,5$ are shown for this major group in Fig. 7, where different base lines are used to indicate the two levels of subdivision. As the fourth major group contains more than one third (36 percent) of the quadrats, sub-

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(13) H.S.X^2 is the abbreviation used for highest single chi-square throughout this account.

TABLE 3 Statistics of major groups.

Major group number	No. of final groups	mean no. of quadrats per final group	SD of mean	% of total no. of quadrats
1	3[a]	15,7	4,9	21,4
2	2[a]	17,0	9,9	15,5
3	4[a]	14,8	10,6	26,7
4	9[b]	8,9	3,6	36,4
4	5[a]	16,0	6,6	36,4

(a) at H.S.X^2 = 15,0

(b) at H.S.X^2 = 7,5

division to a lower level results in groups which are, in general, not much smaller than those in the other major groups (Table 3).

INSERT TABLE 3

There are three final groups in the first major group, two in the second, four in the third and nine in the fourth major group. The mean number of quadrats in the final groups of each major group is given in Table 3. At H.S.X^2 = 15,0 the mean number of quadrats per final group is remarkably similar for the four major groups. The standard deviation of the mean for each major group, however, indicates more variation in number of quadrats per group within the second and third major groups than within the first and fourth groups. At H.S.X^2 = 15,0 the mean number of quadrats per final group is 15,7 with a standard deviation of 0,76. With the finer subdivision of the fourth major group to H.S.X^2 = 7,5, the mean becomes 12,1 (SD = 3,5).

Groups are numbered from 1 to 9 at the H.S.X^2 = 20,0 level and further subdivisions are labelled alphabetically and numerically. Groups are usually referred to in the text by number for brevity although, as was mentioned previously, groups are also named after dominant species and certain habitat features.

2) Re-allocation

Following the procedure described earlier, quadrat 114, originally in Group 3a, was transferred to 4b, quadrat 112 from

3b to 5b, quadrat 152 from 9a to 7a and quadrat 126 from 9c to 9a.

Except where otherwise indicated all results given above and below and including results in all tables and figures relate to groups after re-allocation.

3) Interpretation of major groups

The association analysis did not completely separate Bankenveld from CT Grassland Land Systems. The first two major groups are, however, largely Bankenveld and the last two mainly CT Grassland. Before re-allocation, the first major group consisted of 47 Bankenveld quadrats and no CT Grassland quadrats and the second major group of 34 Bankenveld and two CT Grassland quadrats. After re-allocation, the first two major groups consisted entirely of Bankenveld quadrats.

Thus, the presence of either Schizachyrium sanguineum or Kohautia omahekensis (the first two dividing species) in a quadrat is a good indication of Bankenveld. The absence of these species does not, however, indicate CT Grassland as 29 of the 110 Bankenveld quadrats also contain neither of these species. Nine of the 29 quadrats make up Group 4a, two occur in Group 5a, five in Group 5b, seven in Group 6, four in Group 7c and two in Group 8. The H.S.X^2 division levels indicate that quadrats of the first major group are very distinct and are not related to any quadrats outside Bankenveld. The second major group is almost as distinct. The slight admixture of Bankenveld quadrats in the third and fourth major groups suggests that some Bankenveld quadrats are floristically related to some CT Grassland quadrats but that the reverse does not hold.

4) Final groups

As a separate association analysis of Bankenveld quadrats was carried out, a description is not given of the first two major groups and their final groups and Group 4a, which are made up entirely of Bankenveld quadrats.

a) Group 4b (Short *Stipagrostis uniplumis* Calcareous Grassland)

Group 4b is defined by the absence of *Schizachyrium sanguineum* and *Kohautia omahekensis*, the presence of *Brachiaria serrata* and *Stipagrostis uniplumis* and the absence of *Indigofera daleoides*. It is the first CT Grassland group to be split off. The quadrats form a homogeneous group with regard to species composition and habitat, with the exception of quadrats 194, 161 and 211, which are somewhat aberrant with regard to habitat. As it was not possible to re-allocate these three quadrats by reference to the species in the surrounds, they were retained in the Group.

TABLE 5 Presence percentages of Group 4b (Short Stipagrostis uniplumis Calcareous Grassland) species in descending order of presence (see text for explanation of codes).

Species	Presence	Indicator value	Code symbols
Brachiaria serrata	100		
Stipagrostis uniplumis	100		X
Themeda triandra	100		X
Dicoma anomala	81		
Elionurus argenteus	81		X
Aristida diffusa var. burkei	76	IVS	X
Corchorus asplenifolius	76	IVS	Z
Crabbea angustifolia	76		
Euphorbia inequilatera	76	IVS	
Fingerhuthia africana	71	IVS	Y
Barleria macrostegia	67		
Triraphis andropogonoides	62		
Convolvulus ocellatus var. ornatus	57	IVS	Y
Acalypha sp. (M&E 1267)	48		
Geigeria burkei	48	IVS	Z
Heteropogon contortus	48		
Anthospermum rigidum	43	-IVS	
Thesium costatum	43		Z
Euphorbia sp. (M&B 70)	38	IVS	Z
Selago holubii	33	IVS	Z
Wahlenbergia caledonica	33	IVS	Z
Salvia radula	29	IVS	Z
Scabiosa columbaria	29	IVS	Z
Mariscus capensis	24	IVS	Z

Ecological parameters of Group 4b are summarised in Table 4 and

Table 4 Summarization parameters of Group 4b (Short *Stipagrostis uniplumis* Calcareous Grassland).

Number of quadrats in Group. 21
Mean no. of species per quadrat: 26,3 (SD = 4,9)
Geology: Surface limestone
Geomorphology: Plain
Soil series (after Verster): Lithosol and Soetmelksvlei
Soil depth: 2,5 - 10,0 cm
pH of A-horizon: 7,5
Soil HCl reaction: Strong or moderately-strong
Biotic influence: Grazing light or absent
Mean basal cover: 9,4 percent (total)
3,8 percent (Tall grass stratum: 60 - 90 cm)
5,5 percent (Short grass stratum: 10 - 40 cm)
Notes: a) Many significant positive Indicator values
b) Closely related to Group 6

floristic parameters are given in Table 5.

INSERT TABLE 5

With the exception of quadrats 194 and 211, all quadrats occur on shallow aeolian sand overlying surface limestone. In a few cases the sand deposit is over 30 cm deep, so that the soil may be classified as Soetmelksvlei series, but in general it is a 2,5 to 10 cm deep lithosol. Quadrats 194 and 211 are on deeper soil (> 80 cm) over granite and dolomite, respectively. Quadrat 211 is situated near most of the other quadrats of this Group and is on the ecotone between this and another group. The inclusion of 194 in the Group cannot be explained in terms of either geology or soils. All quadrats are situated on a flat plain with virtually no relief. Soil pH is usually 7,5 but occasionally 7,0 or 8,0. Soil HCl reaction is usually strong or moderately strong in shallow soil and weaker where the soil is deeper. A negative correlation, significant at p = 0,01 was found between soil depth (in cm) and HCl reaction recorded on a 0, 1, 2, 3 intensity scale.

Grazing was light, or absent, for most quadrats of this Group. In about one third of the quadrats selective grazing was observed and in four quadrats (111, 116, 122, 133) heavy grazing and trampling were recorded.

Basal cover data are given in Table 4 together with mean number of species per quadrat. As the overall average number of species per quadrat in CT Grassland is about 24, quadrats of this Group are relatively rich in species.

Species commonly occurring in quadrats of the Group are listed in Table 5. Presence percentage is the number of times a species occurs in the quadrats of the Group, expressed as a percentage of the number of quadrats in the Group. Code X marks species which have high cover-abundance values in many quadrats of the Group and code Y indicates possible indicator species. Indicator species are species which are common within the Group but are uncommon through the rest of the study area. All species with a presence greater than 39 percent are listed and species with lower presence but positive, significant Indicator values (IVS) are also included in Table 5. Code Z marks species which are listed in the floristic summary of this Group but no other group. Although possibly present in one, or a few quadrats of other groups, these species are not common enough to be included in the floristic summary of another group. Where available, they are given for each group as species with limited distributions.

Brachiaria serrata, Stipagrostis uniplumis and Themeda triandra occur in all 21 quadrats of the Group. Possible indicator species include Fingerhuthia africana and Convolvulus ocellatus var. ornatus, although the latter is present in only 12 of the quadrats of the Group.

b) Group 5b (Elionurus argenteus Secondary Grassland)

Group 5 is defined by the absence of Schizachyrium sanguineum and Kohautia omahekensis, the presence of Brachiaria serrata and the absence of Stipagrostis uniplumis. At H.S.X^2 = 18,5 this Group is split on Bulbostylis burchellii into Groups 5a and 5b. As Group 5a contains only three quadrats, two from Bankenveld and one from CT Grassland, it is not considered further. At H.S.X^2 = 13,6 Group 5b splits into a positively-defined group of four Bankenveld and one CT Grassland quadrats and a negatively-defined group of one Bankenveld and 20 CT Grassland quadrats on the presence or absence of Eragrostis stapfii. As Group 5b with E. stapfii is small and made up predominantly of Bankenveld quadrats it is not discussed. The following discussion refers to the 20 CT Grassland quadrats of Group 5b without E. stapfii together with quadrat 112

TABLE 7 Presence percentages of Group 5b (Elionurus argenteus Secondary Grassland) species in descending order of presence (see text for explanation of codes).

Species	Presence	Indicator value	Code symbols
Brachiaria serrata	100		
Heteropogon contortus	95		
Themeda triandra	95		
Elionurus argenteus	90		X
Anthospermum rigidum	85		
Justicia anagaloides	85		
Setaria flabellata	85		
Aristida congesta	70		
Crabbea angustifolia	70		
Barleria macrostegia	65		
Eragrostis curvula	65		
Triraphis andropogonoides	65		
Aristida diffusa var. burkei	60		
Dicoma anomala	55		
Cymbopogon plurinodis	50		
Hibiscus microcarpus	50	IVS	
Lasiosiphon capitatus	50	IVS	Z
Vernonia oligocephala	50	IVS	
Digitaria argyrograpta	45		
Gazania krebsiana	45		
Eragrostis gummiflua	40	IVS	
Chascanum hederaceum	40		Z
Aristida canescens	35	IVS	
Helichrysum zeyheri	30	IVS	Z

re-allocated to this Group. The one Bankenveld quadrat classified to this Group is mentioned where applicable. Ecological parameters of Group 5b are summarised in Table 6 and floristic parameters are

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Table 6 Summarization parameters of Group 5b (Elionurus argenteus Secondary Grassland).

Number of quadrats in Group: 21

Mean number of species per quadrat: 26,5 (SD = 5,2)

Geology: Ventersdorp System

Geomorphology: Plain or crest of hill

Soil series (after Verster): Soetmelksvlei

Soil depth: 15 - 80 cm

pH of A-horizon: 6,5

Soil HCl reaction: absent

Biotic influence: Light or heavy grazing. Signs of soil erosion in some quadrats

Mean basal cover: 8,4 percent (total)
2,2 percent (Tall grass stratum: 60 - 90 cm)
6,3 percent (Short grass stratum: 10 - 40 cm)

Notes: a) Heterogeneous group
b) Few common species with significant Indicator values
c) Similar to Group 8

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given in Table 7.

INSERT TABLE 7

As Group 5b is the last group of the third major group of the hierarchy, a certain amount of heterogeneity in floristics as well as in habitat is expected. Heterogeneity will be apparent from the description which follows.

Quadrats of this Group occur in three main clusters north-west, north-east and south of Lichtenburg, respectively. The clustering is probably due to the sampling method, which resulted in quadrats being located in clusters. The Group is mapped with Group 8.

Various geological substrates underlie quadrats of this Group. Half are underlain by Ventersdorp lava, quartzites, breochia or conglomerate, four are on deep sand overlying dolomite and chert of the Transvaal system and two quadrats each are found on surface limestone, Archaean granite and Dwyka tillite. Three quadrats face north on very gentle slopes and the others occur on flat plains or crests of hills.

Half the quadrats in this Group have soil over 80 cm deep and the rest are on shallower soil with an average depth of 15 cm. All quadrats are found on Soetmelksvlei soil series. Soil pH is usually 6,5 but values of 6,0 or 7,0 are occasionally recorded.

Biotic influence varied widely. Some quadrats were only lightly grazed while others were heavily grazed and some showed signs of soil erosion. All heavily-grazed quadrats were located on deep soil while only light grazing was recorded on shallow soils.

Mean total basal cover was slightly lower than in Group 4b and mean number of species per quadrat was almost the same in both groups.

Species commonly occurring in quadrats of Group 5b are listed in Table 7. Only Brachiaria serrata occurs in all quadrats.

Elionurus argenteus, after which the Group is named, is the only species with high cover-abundance in many quadrats of the Group. No species with high presence percentage have significant Indicator values. Only three species (Code Z: Table 7) are not recorded in the floristic summary of any other group.

c) Group 6 (Tall Stipagrostis uniplumis Calcareous Grassland)

Group 6 is a small group of 13 quadrats defined by the absence of Schizachyrium sanguineum, Kohautia omahekensis and Brachiaria serrata and the presence of Stipagrostis uniplumis. As the only difference in definition between this Group and Group 4, as a whole, is the presence or absence of Brachiaria serrata, a degree of similarity between the two Groups would be expected and, in fact, the Groups do have many features in common. None of the quadrats of Group 6, however, have B. serrata recorded from the surround so they could not be moved to Group 4b on those grounds. Groups 4b and 6 are mapped together, the distribution being given in the description of Group 4b. At H.S.X^2 = 8,0 Group 6 is split on the presence or absence of Vernonia oligocephala into 6a, containing six Bankenveld and one CT Grassland quadrats. The Bankenveld quadrats of Group 6 fall neatly into Group 6 of the Bankenveld analysis discussed later. The six CT Grassland quadrats of Group 6 are considered together even though they are split on Vernonia oligocephala into a group of five quadrats and a single quadrat (113). As the Group is small and similar to Group 4b, the following discussion

TABLE 9 Presence percentages of Group 6 (Tall Stipagrostis uniplumis Calcareous Grassland) species in descending order of presence (A) and presence percentages of species in over 70% of Bankenveld Group 6 quadrats (B) (see text for explanation).

Species	A Presence	Code symbols (for A)	B Presence
Stipagrostis uniplumis	100	X	100
Aristida congesta	83		86
Themeda triandra	83	X	71
Vernonia oligocephala	83		
Anthospermum rigidum	67		
Barleria macrostegia	67		
Elionurus argenteus	67		
Eragrostis superba	67		
Convolvulus ocellatus var. ornatus	50		
Fingerhuthia africana	50		
Hermannia betonicifolia	50	Z	
Nolletia ciliaris	50	Z	
Commelina africana & C. erecta			100
Eragrostis lehmanniana			86
Sporobolus africanus			86
Chascanum pinnatifidum			71
Cymbopogon plurinodis			71
Diplachne fusca			71
Hermannia tomentosa			71
Oropetium capense			71

is short. Ecological parameters of Group 6 are summarized in Table 8

Table 8 Summarization parameters of Group 6 (Tall *Stipagrostis uniplumis* Calcareous Grassland).

Number of quadrats in Group: 6
Mean no. of species per quadrat: 26,3 (SD = 7,4)
Geology: Surface limestone
Geomorphology: Plain
Soil series (after Verster): Soetmelksvlei
Soil depth: 0 - 50 cm
pH of A-horizon: 7,0 - 7,5
Soil HCl reaction: Slight or absent
Biotic influence: Light grazing
Mean basal cover: 13,7 percent (total)
8,0 percent (Tall grass stratum: 60 - 90 cm)
5,7 percent (Short grass stratum: 10 - 40 cm)
Notes: a) Related to Group 4b

and floristic parameters are given in Table 9.

INSERT TABLE 9

All the quadrats are located west of Lichtenburg, some near the town and some as far as 25 km away. All but one of the quadrats occur on flat plains underlain by surface limestone deposits. Slope is negligible and sites are very exposed. Quadrat 210 occurs on a flat plain where sand, over 100 cm deep, overlies dolomite and gravels of the Transvaal System.

Soil over the limestone is sandy and usually 30 to 50 cm deep.

Soil pH is 7,0 or 7,5 and soil HCl reaction is slight or absent.

Grazing was usually light and average total basal cover for both strata was 13,7 percent.

While Stipagrostis uniplumis is the only species occurring in all six CT Grassland quadrats of Group 6 (Table 9), the Group is too small for any Indicator values to be significant. Both Stipagrostis uniplumis and Themeda triandra reach high cover-abundance values in quadrats of this Group. Hermannia betonicifolia is the only species which is not included in the floristic description of any other group.

The Bankenveld section of Group 6 contains a different assemblage of species, adding further weight to the decision to separate the Bankenveld and CT Grassland quadrats of this Group. Species occurring in over 70 percent of the quadrats of the Bankenveld Group are also given in Table 9. Of these, only Aristida congesta, Stipagrostis uniplumis and Themeda triandra occur commonly in CT Grassland quadrats of the Group as well.

d) Group 7

Group 7 is defined by the absence of Schizachyrium sanguineum, Kohautia omahekensis, Brachiaria serrata and Stipagrostis uniplumis and the presence of Crabbea angustifolia. At H.S.X^2 = 12,0 the Group is split on the presence or absence of Hermannia depressa and at H.S.X^2 = 10,8 the positively-defined group is divided on Blepharis integrifolia. The first 15 quadrats, defined by the presence of both H. depressa and B. integrifolia, form a distinct Group, 7a, made up entirely of CT Grassland quadrats. The Group defined by the absence of B. integrifolia, 7b, contains only three quadrats and as it appears related to Group 7c, it is discussed with it. Group 7c, containing four Bankenveld and five CT Grassland quadrats, is defined by the absence of both the above-mentioned dividing species.

i) Group 7a (Cymbopogon plurinodis Grassland)

Only one quadrat (120) appears mis-classified in this Group. As it could not be re-allocated by reference to the species in the surround, it was left in the Group. Quadrat 152 was re-allocated to this Group from 9a. Ecological parameters of Group 7a are summarised in Table 10

Table 10 Summarization parameters of Group 7a (Cymbopogon plurinodis Grassland).

Number of quadrats in Group: 15
Mean no. of species per quadrat: 26,4 (SD = 4,5)
Geology: Dwyka tillite
Geomorphology: Plain
Soil series (after Verster): Soetmelksvlei
Soil depth: 100 cm
pH of A-horizon: 7,5 - 8,0
Soil HCl reaction: slight or absent
Biotic influence: Range from total protection to heavy grazing
Mean basal cover: 9,1 percent (total)
2,7 percent (Tall grass stratum: 60 - 90 cm)
6,4 percent (Short grass stratum: 10 - 40 cm)

TABLE 11 Presence percentages of Group 7a (*Cymbopogon plurinodis* Grassland) species in descending order of presence (see text for explanation of codes).

Species	Presence	Indicator value	Code symbols
Blepharis integrifolia	100		
Hermannia depressa	100		
Themeda triandra	100		
Barleria macrostegia	93		
Crabbea angustifolia	93		
Elionurus argenteus	87		X
Eragrostis curvula	87		
Cymbopogon plurinodis	80		X
Eustachys mutica	80		
Setaria flabellata	80		
Aristida canescens	73		X
Anthospermum rigidum	73		
Eragrostis superba	73		
Gazania krebsiana	67	IVS	
Aristida congesta	67		
Helichrysum caespititium	67		Z
Eragrostis lehmanniana	60	IVS	
Hibiscus pusillus	60	IVS	
Triraphis andropogonoides	60		
Felicia muricata	53	IVS	
Euphorbia inequilatera	53		
Crabbea hirsuta	53	IVS	Z
Corchorus asplenifolius	47		
Digitaria argyrograpta	47		
Eragrostis stapfii	47		
Euphorbia pseudotuberosa	47	IVS	Z
Justicia anagaloides	40		
Rhynchosia totta	40		

and floristic parameters are given in Table 11.

INSERT TABLE 11

Quadrats of this Group occur in two clusters near each other. One cluster borders Lichtenburg to the south-east and the other is east of the town. Two large areas and a number of small fields are mapped as Group 7a, where quadrats of this Group are located.

With the exception of quadrat 120, quadrats of this Group are located on flat plains underlain by Dwyka tillite. Slope is one percent or less and sites are exposed. The soil series in all quadrats is Soetmelksvlei. Average depth is about one metre and soil pH is 7,5 or 8,0. A slight soil HCl reaction is occasionally recorded.

Quadrat 120 occurs in a slight hollow on a flat plain covered with surface limestone. The soil series is Arcadia or Muden. Soil depth is 40 cm with a pH of 7,5 and no soil HCl reaction.

Within Group 7a, biotic influence was most variable. Some quadrats enjoyed total protection from grazing, as within the Lichtenburg aerodrome reserve, while others in the municipal commonage were heavily grazed and trampled.

All species with a presence exceeding 39 percent in quadrats of Group 7a are listed in Table 11. Blepharis integrifolia, Hermannia depressa and Themeda triandra occur in all 15 quadrats. High cover-abundance values were recorded for Elionurus argenteus, Cymbopogon plurinodis and Aristida canescens. Helichrysum caespititium, Euphorbia pseudotuberosa and Crabbea hirsuta are not common enough to be included in the floristic summary of any other Group.

Cymbopogon plurinodis has a high cover-abundance rating in 80 percent of the quadrats of the Group. It has neither a high cover-abundance rating nor significant Indicator value in any other group. As the next commonest species, Elionurus argenteus, had a high cover-abundance rating in only 43 percent of the quadrats, this species is not included in the name of the Group.

ii) Groups 7b and 7c

Quadrats of Groups 7b and 7c occur scattered through the study area. Ecological parameters of CT Grassland quadrats of these Groups are summarized in Table 12 and floristic parameters are

Table 12 Summarization parameters of Groups 7b and 7c.

Number of quadrats in combined Groups: 8
Mean no. of species per quadrat: 23,6 (SD = 3,1)
Geology: Various substrates
Geomorphology: Plain
Soil series (after Verster): Soetmelksvlei
Soil depth: 35 - 100 cm
pH of A-horizon: 6,0 - 7,0
Soil HCl reaction: absent
Biotic influence: Light grazing
Mean basal cover: 7,5 percent (total)
2,0 percent (Tall grass stratum: 60 - 90 cm)
5,5 percent (Short grass stratum: 10 - 40 cm)

Notes: a) Groups not mapped as very small and quadrats scattered throughout area

TABLE 13 Presence percentages of Groups 7b and 7c species in descending order of presence (see text for explanation of codes).

Species	Presence	Code symbols
Crabbea angustifolia	100	
Themeda triandra	100	X
Anthospermum rigidum	88	
Triraphis andropogonoides	88	
Aristida congesta	75	
Cymbopogon plurinodis	75	
Eragrostis curvula	75	
Heteropogon contortus	75	X
Justicia anagaloides	63	
Setaria flabellata	63	X
Vernonia oligocephala	63	
Acalypha sp. (M&E 1267)	50	
Barleria macrostegia	50	
Cassia mimosoides	50	Z
Cynodon dactylon	50	
Diplachne fusca	50	Z
Elionurus argenteus	50	X
Eustachys mutica	50	
Hypoxis sp.	50	Z

summarised in Table 13. The quadrats are found on a number of

INSERT TABLE 13

geological substrates and soil series. Three quadrats are located on surface limestone (Soetmelksvlei soil series), three on sand overlying dolomite and gravels (Soetmelksvlei series), one on granite and one on Ventersdorp brecchia and conglomerate. All are on exposed, flat sites.

In most quadrats, grazing was light or the vegetation had been rested for some time before sampling. Heavy grazing was recorded from two quadrats.

Species occurring in more than three of the eight CT Grassland quadrats of these Groups are listed in Table 13. Only two species, Crabbea angustifolia and Themeda triandra occur in all eight quadrats and three species have high cover-abundance estimates in most quadrats of the Groups. The combined Group is too small for any Indicator values to be significant.

The two Groups described above do not form distinct, mappable units. As a number of quadrats apparently belonging to other Groups appear to be included in these Groups and as they are small they are neither mapped nor named.

e) Group 8 (Elionurus argenteus Primary Grassland)

Group 8 is defined by the absence of Schizachyrium sanguineum, Kohautia omahekensis, Brachiaria serrata, Stipagrostis uniplumis

TABLE 15 Presence percentages of Group 8 (Elionurus argenteus Primary Grassland) species in descending order of presence (see text for explanation of code).

Species	Presence	Code symbol
Heteropogon contortus	100	
Anthospermum rigidum	89	
Aristida congesta	89	
Eragrostis curvula	89	
Setaria flabellata	89	
Themeda triandra	78	
Elionurus argenteus	67	X
Barleria macrostegia	67	
Digitaria argyrograpta	67	
Eustachys mutica	67	
Hibiscus microcarpus	67	
Triraphis andropogonoides	67	
Diplachne fusca	56	
Eragrostis gummiflua	56	
Hermannia betonicifolia	56	
Lasiosiphon capitatus	56	
Pogonarthria squarrosa	56	
Cymbopogon excavatus	44	
Gazania krebsiana	44	
Helichrysum caespititium	44	
Hermannia depressa	44	
Justicia anagaloides	44	
Nolletia ciliaris	44	
Raphionacme hirsuta	44	

and Crabbea angustifolia and the presence of Heteropogon contortus. It is a small group of 11 quadrats, nine of which are within CT Grassland. Ecological parameters of the CT Grassland Group are summarised in Table 14 and floristic parameters are summarised

Table 14 Summarization parameters of Group 8 (Elionurus argenteus Primary Grassland).

Number of quadrats in Group: 9
Mean no. of species per quadrat: 23,1 (SD = 4,4)
Geology: Mostly Ventersdorp system
Geomorphology: Plain or gentle waxing slope
Soil series (after Verster): Soetmelksvlei
Soil depth: 60 - >100 cm
pH of A-horizon: 6,5 - 7,0
Soil HCl reaction: absent
Biotic influence: Light grazing or none at all. Vegetation in good condition
Mean basal cover: 10,4 percent (total)
4,0 percent (Tall grass stratum: 60 - 90 cm)
6,4 percent (Short grass stratum: 10 - 40 cm)
Notes: a) High cover-abundance values rare
b) Related to Group 5b

in Table 15. Quadrats of this Group occur mainly at two places,

INSERT TABLE 15

east of and west of Lichtenburg, respectively. The Group is mapped with Group 5b.

Five quadrats occur on Ventersdorp conglomerate, lava or quartzites, three on sand overlying dolomite and gravels and one on Dwyka tillite. Quadrats are on extensive flat plains or on gentle waxing slopes.

The soils developed from the three rock types all belong to Soetmelksvlei series. Soils are usually 60 cm to over one metre deep, soil pH is usually between 6,5 and 7,0 and no soil HCl reaction is recorded.

With only one exception, the quadrats of this Group were not grazed or were only lightly grazed and in good condition.

Species present in more than 39 percent of the quadrats of Group 8 are listed in Table 15. Heteropogon contortus is the only species occurring in all 9 quadrats of this Group. The Group is too small for any Indicator values to be significant.

High cover-abundance values were only rarely recorded for species in quadrats of this Group. In addition to the common grass Elionurus argenteus, Eragrostis gummiflua and Eustachys mutica were the only species with high cover-abundance values in three or more quadrats.

f) Group 9

At $H.S.X^2 = 20,0$, Group 9 is the last group of the analysis. It is defined by the absence of all dividing species, namely:-

Schizachyrium sanguineum, Kohautia omahekensis, Brachiaria serrata, Stipagrostis uniplumis, Crabbea angustifolia and Heteropogon contortus. No Bankenveld Land System quadrats occur in Group 9.

Twelve quadrats, defined by the presence of Triraphis andropogonoides, are split off Group 9 at H.S.X^2 = 16,0 to form Group 9a. Two slightly different subgroups are recognised within 9a. The first subgroup, 9ai, of nine quadrats, is defined by the presence of Dicoma macrocephala or the presence of both D. macrocephala and Digitaria argyrograpta. The second subgroup, 9aii, containing three quadrats, is defined by the absence of both these species. Group 9b is defined by the absence of Triraphis andropogonoides and the presence of Barleria macrostegia. Ten quadrats are contained in the Group. The seven quadrats of Group 9c are defined by the absence of both the above dividing species. Group 9c is the last group of the analysis and is defined entirely on the absence of dividing species.

Quadrat 126 was re-allocated from Group 9c to the first subgroup of 9a and quadrat 152 was re-allocated from the first subgroup of 9a to Group 7a on the bases of species recorded in the surrounds of these quadrats.

Subgroups of Group 9 have a number of features in common. Most of the quadrats are on Ventersdorp system rocks. The soil is usually deep with a pH of 6,0 or 7,0. In nearly all quadrats, grazing was heavy and trampling was recorded. Grass basal cover was low and the mean number of species per quadrat was about 20, the lowest of any group of the analysis.

i) Group 9a (Acacia karroo Savanna and Secondary Cymbopogon plurinodis Grassland).

Ecological parameters of Group 9ai, named Acacia karroo Savanna, are summarised in Table 16 and ecological parameters of Group 9aii,

Table 16 Summarization parameters of Group 9ai (Acacia karroo Savanna).

Number of quadrats in Group: 9
Mean no. of species per quadrat: 21,8 (SD = 5,2)
Geology: Ventersdorp quartzites or sand over granite
Geomorphology: Plain or waning slope
Soil series (after Verster): Lichtenburg, Soetmelksvlei and Rensburg
Soil depth: 90 cm
pH of A-horizon: 6,0 - 7,0
Soil HCl reaction: absent
Biotic influence: Heavy grazing and trampling
Mean basal cover: 6,3 percent (total)
1,7 percent (Tall grass stratum: 60 - 90 cm)
4,5 percent (Short grass stratum: 10 - 40 cm)
Notes: a) Trees invading grassland
b) Early stage in succession to A. karroo Open Woodland

which is related to Group 7a and named Secondary Cymbopogon plurinodis Grassland, are summarised in Table 17.

Table 17 Summarization parameters of Group 9aii (Secondary Cymbopogon plurinodis Grassland).

Number of quadrats in Group: 3
Mean no. of species per quadrat: 22,0 (SD = 11,0)
Geology: Dwyka tillite
Geomorphology: Plain or gentle waxing slope
Soil series (after Verster): Soetmelksvlei
Soil depth: 30 - 90 cm
pH of A-horizon: 7,0 - 7,5
Soil HCl reaction: absent
Biotic influence: Heavy grazing and trampling, vegetation in poor condition
Mean basal cover: 8,3 percent (total)
2,8 percent (Tall grass stratum: 60 - 90 cm)
5,5 percent (Short grass stratum: 10 - 40 cm)
Notes: a) Group too small for accurate description
b) Mapped with Group 7a

Quadrats of Group 9a occur scattered through the area east of Lichtenburg. Four quadrats occur in a cluster of Group 9c quadrats. One quadrat (126), which was re-allocated to this Group, occurs west of Lichtenburg and it differs from the rest of the Group in other respects as well. A small area of Group 9ai, not containing any quadrats, is mapped to the south of Lichtenburg and Group 9aii is mapped with Group 7a.

Quadrats of the first subgroup of Group 9a occur on Ventersdorp

TABLE 18 Presence percentages of Group 9ai (Acacia karroo Savanna) species in descending order of presence (see text for explanation of code).

Species	Presence	Code symbols
Aristida congesta	100	
Digitaria argyrograpta	89	
Eustachys mutica	89	X
Themeda triandra	89	
Triraphis andropogonoides	89	X
Blepharis integrifolia	78	
Eragrostis gummiflua	78	X
Eragrostis lehmanniana	78	X
Eragrostis superba	78	
Solanum supinum	78	
Eragrostis curvula	67	X
Lippia scaberrima	67	
Sporobolus africanus	67	
Hermannia depressa	56	
Setaria flabellata	56	
Thesium costatum	56	
Anthospermum rigidum	44	
Cymbopogon plurinodis	44	
Cynodon dactylon	44	X
Dicoma macrocephala	44	
Justicia anagaloides	44	

quartzites while those of the second subgroup are found on Dwyka tillite substrate. Quadrat 126, the aberrant, re-allocated quadrat, occurs on a surface limestone deposit. Quadrats of the first subgroup occur on extensive flat plains or on waning slopes to streams while those of the second subgroup occur on flat plains or waxing slopes. In all cases, slopes are very slight (one degree or less). About half the quadrats are moderately-exposed and half are exposed.

A number of soil series are represented in the first subgroup, including Lichtenburg, Soetmelksvlei and Rensburg, while all three quadrats of the second subgroup are on Soetmelksvlei series. Soils are relatively deep, averaging about 90 cm. Soil pH varies between 6,0 and 7,0 and no soil HCl reaction is recorded.

In all the quadrats of this Group, grazing was heavy and the vegetation had been trampled. Trees were invading grassland at a number of Group 9ai sites. The most common tree was _Acacia karroo_, which occurred as a seedling or full-grown tree up to 4 m tall. _Ziziphus mucronata_ occurred occasionally as well as the following shrubs:- _Asparagus laricinus_, _Diospyros lycioides_ and _Maytenus heterophylla_.

Basal cover was low in quadrats of Group 9ai. Average total basal cover was only 6,3 percent. Mean number of species per quadrat in both subgroups was about 22,0.

Species present in more than 39 percent of the quadrats of Group 9ai are listed in Table 18. _Aristida congesta_ is the only

INSERT TABLE 18

TABLE 19 Presence percentages of Group 9aii (Secondary *Cymbopogon plurinodis* Grassland) species in descending order of presence (see text for explanation of code).

Species	Presence	Code symbols
Barleria macrostegia	100	
Blepharis integrifolia	100	
Cymbopogon plurinodis	100	X
Elionurus argenteus	100	X
Eragrostis curvula	100	X
Eustachys mutica	100	X
Themeda triandra	100	
Triraphis andropogonoides	100	X
Aristida congesta	67	
Eragrostis lehmanniana	67	X
Euphorbia inequilatera	67	
Hermannia depressa	67	
Hibiscus pusillus	67	
Setaria flabellata	67	
Solanum supinum	67	

species occurring in all quadrats of the Group. Six species have high cover-abundance estimates in most quadrats of the Group.

Species present in more than one of the three quadrats of Group 9aii are listed in Table 19. As there are only three

INSERT TABLE 19

quadrats in the Group, these presence values can hardly be relied on.

Both Groups 9ai and 9aii are too small for any Indicator values to be significant. Species which are more common in Group 9ai than Group 9aii include: Digitaria argyrograpta, Eragrostis gummiflua, E. superba, Lippia scaberrima and Sporobolus africanus. As Group 9aii is so small, species presence in it are not known accurately. The following species, however, appear more common in Group 9aii than in 9ai:- Cymbopogon plurinodis, Elionurus argenteus, Euphorbia inequilatera, Hermannia depressa, Hibiscus pusillus and Setaria flabellata.

ii) Group 9b (Acacia karroo Open Woodland)

Quadrats of this Group are distributed in two clusters, south and south-east of Lichtenburg, respectively. Relatively large areas south and south-east of Lichtenburg are mapped as Group 9b. Ecological parameters of Group 9b are summarised in Table 20.

Table 20 Summarization parameters of Group 9b (Acacia karroo Open Woodland).

Number of quadrats in Group: 10

Mean no. of species per quadrat: 20,7 (SD = 2,1)

Geology: Ventersdorp System

Geomorphology: Plain or crest of rise

Soil series (after Verster): Soetmelksvlei and Lichtenburg

Soil depth: 60 - 100 cm

pH of A-horizon: 6,0 - 6,5

Soil HCl reaction: absent

Biotic influence: Heavy grazing and trampling

Mean basal cover: 5,4 percent (total)
1,0 percent (Tall grass stratum: 60 - 90 cm)
4,4 percent (Short grass stratum: 10 - 40 cm)

Notes: a) Tree species may be common

Nine of the ten quadrats of this Group are situated on Ventersdorp System rocks. Ventersdorp lava, conglomerate, brecchia and quartzites are represented. The remaining quadrat is located on granite. Most of the quadrats are located on flat plains or the crests of hills where slope is too slight to measure. Most of the quadrats are sheltered or moderately sheltered, in marked contrast to the quadrats of other groups described above. Sheltering is usually by the presence of trees in, or near, the quadrats.

Soetmelksvlei series, Soetmelksvlei lithosol and Lichtenburg series are the most common soils recorded for these quadrats. Soil is usually 60 cm to one metre deep with a pH of 6,0 to 6,5.

TABLE 21 Presence percentages of Group 9b (Acacia karroo Open Woodland) species in descending order of presence (see text for explanation of code).

Species	Presence	Indicator value	Code symbols
Barleria macrostegia	100		
Felicia muricata	90		
Cynodon dactylon	90		X
Lippia scaberrima	90		
Sporobolus africanus	90		X
Aristida congesta	80		
Eragrostis superba	80		
Blepharis integrifolia	70		
Eragrostis curvula	70		X
Solanum supinum	70		
Themeda triandra	60		
Brayulinea densa	50	IVS	
Eragrostis lehmanniana	50		
Lasiocorys capensis	50	IVS	
Anthospermum rigidum	40		
Antizoma angustifolia	40		
Cymbopogon plurinodis	40		
Digitaria argyrograpta	40		
Elionurus argenteus	40		
Hermannia depressa	40		
Hibiscus pusillus	40		
Setaria flabellata	40		

Nearly all the quadrats showed signs of heavy grazing and trampling. The condition of the vegetation of even those quadrats in which grazing appeared moderate was recorded as being poor, probably as a result of heavy grazing in the past.

Basal cover in quadrats of this Group was low. Total average basal cover was only 5,4 percent. The number of species per quadrat was also low, the average being 20,7, and 24 being the highest number of species recorded in a quadrat of the Group.

Species present in more than 39 percent of the quadrats of Group 9b are listed in Table 21. Barleria macrostegia is the only

INSERT TABLE 21

species occurring in all ten quadrats. Brayulinea densa and Lasiocorys capensis have significant Indicator values. High cover-abundance was recorded for three species in the Group. Trees and shrubs are recorded from the surrounds of six quadrats. The most common tree is Acacia karroo, which attains a height of 4,5 to 6 m. Occasional, or co-dominant with A. karroo is A. caffra. Other trees found occasionally include Celtis africana (7,5 m), Ziziphus mucronata (5,5 m), Acacia robusta (rare) and Rhus lancea. In Acacia karroo Open Woodland the trees are usually one to three crown-diameters apart.

Shrubs include Maytenus heterophylla, which can encroach on shallow soil with mismanagement, Xeromphis rudis, Grewia flava (occasional, or common, in understorey), Asparagus laricinus and Diospyros lycioides.

iii) Group 9c (Drainage Basin *Acacia karroo* Open Woodland)

Six quadrats of this Group are located east of Lichtenburg along a tributary of the Harts River. The other quadrat (183) occurs south-east of Lichtenburg with quadrats of Groups 9a and 9b. Although the bed of the Harts River was not sampled, the whole drainage basin is mapped as Group 9c, pending more detailed investigation. Ecological parameters of Group 9c are summarised in Table 22.

Table 22 Summarization parameters of Group 9c (Drainage basin *Acacia karroo* Open Woodland).

Number of quadrats in Group: 7
Mean no. of species per quadrat: 15,2 (SD = 3,7)
Geology: Ventersdorp series quartzites
Geomorphology: Plain or waning slope to drainage line
Soil series (after Verster): Rensburg and Rensburg or Soetmelksvlei
Soil depth: 100 cm
pH of A-horizon: 6,0 - 7,0
Soil HCl reaction: usually absent
Biotic influence: Heavy grazing and trampling
Mean basal cover: 6,2 percent (total)
1,6 percent (Tall grass stratum: 60 - 90 cm)
4,6 percent (Short grass stratum: 10 - 40 cm)
Notes: a) Group defined by absence of all dividing species
b) Variety of tree species present

TABLE 23 Presence percentages of Group 9c (Drainage Basin _Acacia karroo_ Open Woodland) species in descending order of presence (see text for explanation of codes).

Species	Presence	Code symbols
Digitaria argyrograpta	86	X
Blepharis integrifolia	71	
Cynodon dactylon	71	
Eragrostis curvula	71	X
Setaria flabellata	71	
Sporobolus africanus	71	
Themeda triandra	71	X
Panicum coloratum	71	Z
Eragrostis lehmanniana	57	
Eustachys mutica	57	
Hibiscus pusillus	57	
Acacia karroo	43	Z
Aptosimum indivisum	43	Z
Aristida congesta	43	
Felicia muricata	43	

The geological formation underlying all the quadrats is Ventersdorp series quartzites. Two quadrats are on flat plains, four on waning slopes to drainage lines and one is in a drainage basin. Most quadrats are north-facing on gentle slopes. Four of the quadrats are sheltered by trees in and near them.

A number of soil series are represented in this Group. Three quadrats are on Rensburg series alluvial clay, two on the transition between Rensburg and Soetmelksvlei series and two on Lichtenburg series. Soils are usually one metre deep and pH varies between 6,0 and 7,0. Soil HCl reaction is recorded from two quadrats.

Heavy grazing and trampling were recorded for five of the quadrats but in two quadrats the vegetation was in good condition and grazing had been light.

Total basal cover was low (6,2 percent), but slightly higher than in Group 9b. Mean number of species per quadrat was 15,2, a low value for the vegetation of the study area, with the least being 12 and the most being 21 species per quadrat.

Species present in more than 39 percent of the quadrats of Group 9c are listed in Table 23. Digitaria argyrograpta, in six

INSERT TABLE 23

of the seven quadrats, is the most common species. Digitaria argyrograpta, Eragrostis curvula and Themeda triandra reach high cover-abundance estimates in quadrats of the Group. Three species are not listed as present in any other group of the analysis.

Trees and shrubs, similar to those of Group 9b, were recorded

TABLE 24 Presence percentages of combined Groups 9b and 9c species in descending order of presence (see text for explanation of code).

Species	Presence	Indicator value	Code symbols
Cynodon dactylon	82		X
Sporobolus africanus	82		X
Felicia muricata	71	IVS	
Blepharis integrifolia	71		
Eragrostis curvula	71		X
Aristida congesta	65		
Themeda triandra	65		
Barleria macrostegia	59		
Digitaria argyrograpta	59	IVS	
Lippia scaberrima	59	IVS	
Eragrostis lehmanniana	53		
Eragrostis superba	53		
Setaria flabellata	53		
Solanum supinum	53	IVS	
Hibiscus pusillus	47	IVS	
Eustachys mutica	41		
Panicum coloratum	41	IVS	
Brayulinea densa	35	IVS	

from four quadrats.

iv) Combined Groups 9b and 9c

Individually, Groups 9b and 9c are too small to produce many significant Indicator values. Considering that they are the last Groups of the analysis, however, a surprising number of significant Indicator values are found in the combined Group. Species occurring in more than five of the 17 quadrats of the combined Group are listed in Table 24. Seven species out of 18 have significant Indicator

INSERT TABLE 24

values and three species have high cover-abundance estimates in quadrats of the Group. In addition, Anthospermum rigidum and Lasiocorys capensis, which occur in five of the quadrats, have significant Indicator values.

Bankenveld association analysis

1) Description of hierarchy

The association analysis hierarchy resulting from classification of the 110 Bankenveld Land System quadrats is given in Fig. 8. The first three divisions yield four distinct major

INSERT FIG. 8

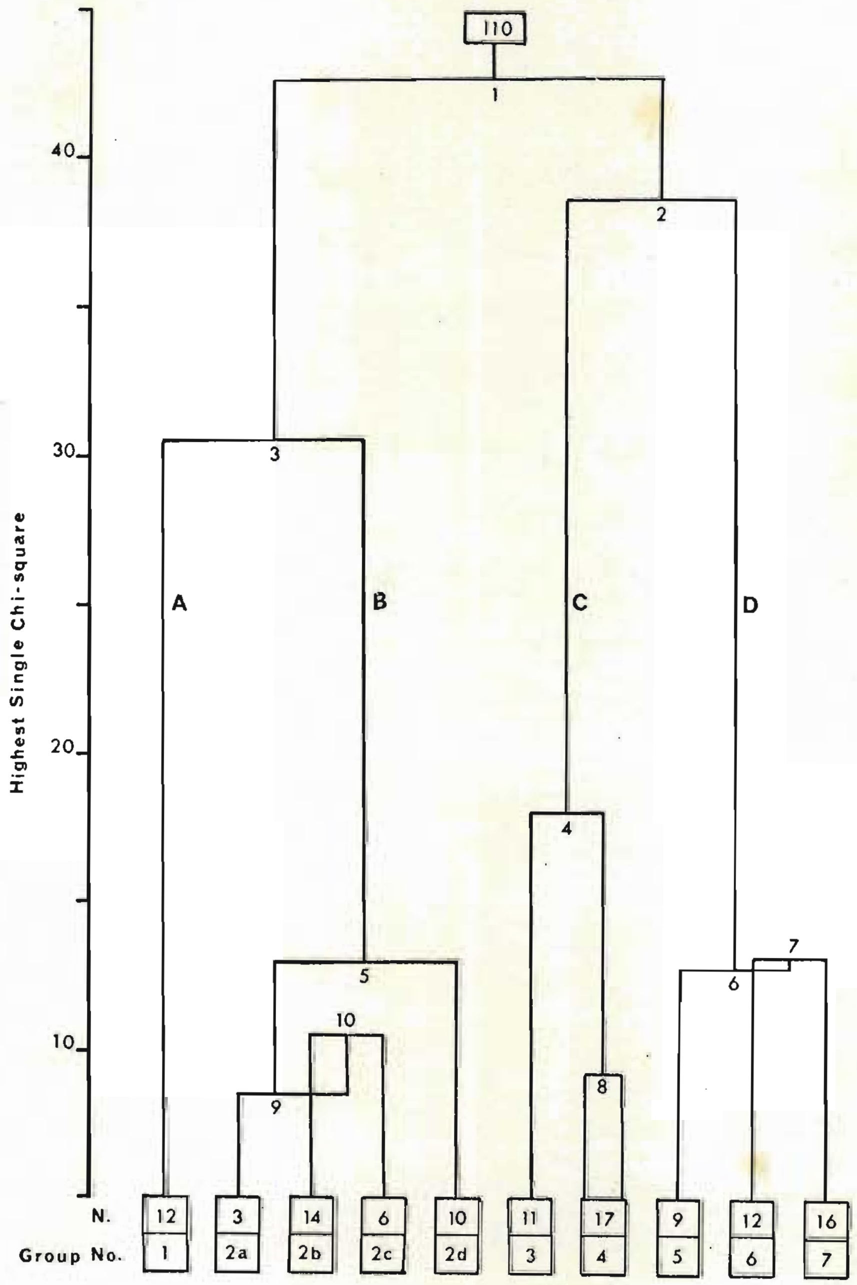

Fig. 8 Association analysis hierarchy of Bankenveld Land System. Dividing species are: 1 = Diheteropogon amplectens, 2 = Chascanum hederaceum, 3 = Stipagrostis uniplumis, 4 = Eragrostis racemosa, 5 = Sporobolus pectinatus, 6 = Ursinia nana, 7 = Oropetium capense, 8 = Schizachyrium sanguineum, 9 = Corchorus asplenifolius, 10 = Heteropogon contortus.

groups, labeled A to D for convenience (Fig. 8). The first Group, A, characterised by the presence of Diheteropogon amplectens and Stipagrostis uniplumis is small, consisting of only 12 quadrats. It is very homogeneous with regard to species associations as it does not divide from H.S.$X^2 > 30,0$ until H.S.$X^2 = 7,2$. In addition to being a major group it is also Final Group 1. Group B contains 33 quadrats and is defined by the presence of Diheteropogon amplectens and the absence of Stipagrostis uniplumis. At H.S.$X^2 = 8,0$ it is divided into four Final Groups, named 2a, 2b, 2c and 2d. Group C contains 28 quadrats and is divided into two Final Groups at H.S.$X^2 = 15,0$. Final Group 3 is defined by the absence of Diheteropogon amplectens and the presence of Chascanum hederaceum and Eragrostis racemosa. Final Group 4, defined by the absence of D. amplectens and E. racemosa and the presence of Chascanum hederaceum, is divided at H.S.$X^2 = 9,3$ on the presence or absence of Schizachyrium sanguineum. Three Final Groups are obtained from major Group D, which is defined by the absence of both D. amplectens and C. hederaceum. Group D contains 37 quadrats. At H.S.$X^2 = 12,7$ Final Group 5 is split off from Group D on the presence of Ursinia nana. Then, at a slightly higher Highest Single Chi-square (13,1), the part of Group D without U. nana is split into Final Groups 6 and 7 on the presence or absence of Oropetium capense. Final Groups in A and B were obtained by terminating division at H.S.$X^2 = 8,0$ and final groups in C and D by terminating division at H.S.$X^2 = 10,0$. These levels were chosen arbitrarily, purely for naming purposes and divisions below H.S.$X^2 = 8,0$ and H.S.$X^2 = 10,0$, respectively, are discussed at appropriate places in the text.

Based on a study of hierarchy division levels ($H.S.X^2$) Groups A and B, on the one hand, are most dissimilar from Groups C and D on the other. Groups C and D differ more from each other than does Group A from B as the former divide further at a higher $H.S.X^2$ than the latter. The small number of splits above $H.S.X^2 = 15,0$, at which level there are only five groups, suggests that the sample consists of a few, large groups, which are rather homogeneous. The homogeneity of A was mentioned above. Major Groups C and D are also homogeneous, the former being maintained from $H.S.X^2 > 35,0$ to $H.S.X^2 = 18,0$ and the latter from $H.S.X^2 > 35,0$ to $H.S.X^2 = 12,7$.

The mean number of quadrats in each final group is fairly constant. Fewest quadrats are found in Final Groups 2a, 2b, 2c and 2d (8,2 average). On average, twelve quadrats are found in each final group of major Groups A and D. The average number of quadrats in Final Groups 3 and 4 is 14,0.

Re-allocation was not required in this analysis and the few quadrats which do not fit the description of a particular group as a whole are discussed in the group description.

2) Species distribution within groups

Lists of species commonly occurring in each final group were drawn up as part of the interpretation of each group. It was found that large numbers of species seemed common to many groups and that there were few species that were restricted to only one or two groups.

To study these findings at greater depth, a species-in-groups

TABLE 25 Presence percentages of species with presence exceeding 39% in all groups defined by the Bankenveld association analysis (See text for explanation of symbols).

Species	Group					
	1	B	3	4	5	6	7
Anthospermum rigidum	100	73	73	88	89	42 -IVS	68
Aristida congesta	73 X	88	91 X	100 X	89	100 X	100 X
Blepharis integrifolia	46	61	73	82	67	42	44
Commelina africana & C.erecta	55	79	82	71	78	92	75
Crabbea angustifolia	100	76	82	82	56	42 -IVS	63
Diplachne fusca	64	88	82	65	67	42	56
Elionurus argenteus	91 X	88	91 X	65 X	44	50	81 X
Themeda triandra	91 X	58 -IVS	100 X	100 X	78 X	75 X	100 X
Triraphis andropogonoides	91 X	52 -IVS	91	94	44	67	75

TABLE 26 Presence percentages of species with presence exceeding 19% in all groups defined by the Bankenveld association analysis (See text for explanation of symbols).

Species	Group						
	1	B	3	4	5	6	7
Anthephora pubescens	82 X	21 -IVS	55	82 X	67 X	67 X	56 X
Aristida diffusa var. burkei	91 X	73 X	55	35	22	42	63 X
Barleria macrostegia	82	49	55	59	56	33	81
Brachiaria serrata	100	91	91	71	44	33	69
Cassia mimosoides	64	55	64	53	22	42	44
Dicoma macrocephala	73	21 -IVS	55	71 IVS	56	42	38
Eragrostis curvula	55	67 X IVS	46 X	24	44	50 X	38
Eragrostis stapfii	64	24 -IVS	36	71	56	33	69
Euphorbia inequilatera	100	36 -IVS	64	82	78	83	38
Pogonarthria squarrosa	82	42 -IVS	64	88	44	33	75
Raphionacme burkei	36	55	64	47	67	25	38

TABLE 27 Presence percentages of species occurring in at least 20% of the quadrats of all but one group of the Bankenveld association analysis (- indicates presence percentage less than 20, see text for explanation of other symbols).

Species	Group						
	1	B	3	4	5	6	7
Chasacanum pinnatifidum	46	-	27	65 IVS	67	50	50
Corchorus asplenifolius	73	-	73	53	100	50	31
Cyperus margaritaceus	27	-	46	35	22	58 IVS	31
Eragrostis superba	27	-	36	41	78	75 X	69 IVS
Eustachys mutica	46	-	36	65 IVS	56	58	38
Indigofera daleoides	55	-	46	65	78	58	75
Setaria flabellata	55	-	55	29	33	33	69 IVS
Stipagrostis uniplumis	100 X	-	27	71 X	78 X	100 X	56 X
Heteropogon contortus	64 X	76	73 X	65 X	-	75	50
Acalypha <u>sp</u>.(M&E 1267)	64	88	55	24	44	-	38
Chaetacanthus costatus	64	61	36	41	33	-	38
Helichrysum caespititium	46	88	64	41	67	-	25
Justicia anagaloides	91	97	100	88	78	-	56 -IVS
Kohautia omahekensis	91	30 -IVS	73	88	89	-	38
Bulbostylis burchellii	55	88	64	24	33	25	-
Cymbopogon excavatus	46	58 X IVS	73 X	35	33	33	-
Ipomoea obscura <u>var</u>. fragilis	55	42	46	41	22	58	-
Ophrestia oblongifolia	55	73 IVS	46	35	22	33	-

TABLE 28 Presence percentages of species occurring in at least 20% of the quadrats of all but two groups of the Bankenveld association analysis (- indicates presence percentage less than 20, see text for explanation of other symbols).

Species	Group 1	B	3	4	5	6	7
Pygmaeothamnus zeyheri	46	49 IVS	46	24	22	-	-
Rhynchelytrum repens	27	27	55 IVS	24	33	-	-
Senecio venosus	82	73 IVS	46	35	22	-	-
Solanum supinum	27	24	55	77	44	-	-
Ursinia nana	55	27	55	71 IVS	100	-	-
Cyphocarpa angustifolia	46	52 IVS	55	29	33	-	-
Gazania krebsiana	64	36	64	41	-	42	-
Oxygonum dregeanum	46	64 IVS	46	-	22	-	25
Crassula transvaalensis	73	49	-	29	44	-	25
Helichrysum cerastioides	46	58	-	53	56	50	-
Vernonia oligocephala	36	-	-	41	33	67	38
Turbina oblongata	55	-	-	29	44	92	56
Hermannia tomentosa	73	-	-	53	78	67	50
Cymbopogon plurinodis	64	-	-	41	33	67	88 X
Eragrostis tricophora	-	-	55 X	53 X	44	33	25
Eragrostis lehmanniana	-	-	36	29	67 X	67	38

TABLE 29 Presence percentages of species in groups defined by the Bankenveld association analysis. Species present in at least 20% of the quadrats of: a) one group, b) two groups, c) three groups and d) four groups (- indicates presence percentage less than 20, see text for explanation of other symbols).

	Species	Group 1	Group B	Group 3	Group 4	Group 5	Group 6	Group 7
a)	Eragrostis gummiflua	-	-	-	-	-	42 IVS	-
	Euphorbia sp. (M&B 70)	-	-	-	-	-	42 IVS	-
	Fingerhuthia africana	-	-	-	-	-	58 X	-
b)	Cynodon dactylon	-	-	-	-	44	25	-
	Mariscus capensis	-	-	27	-	-	42 IVS	-
	Diplachne biflora	-	52 IVS	27	-	-	-	-
	Tephrosia longipes	-	52 IVS	46	-	-	-	-
	Setaria nigrirostris	-	-	-	41 IVS	22	-	-
c)	Elephantorrhiza elephantina	-	49 IVS	36	-	-	-	31
	Lippia scaberrima	-	-	46 IVS	-	22	25	-
	Menodora africana	27	-	-	41 IVS	22	-	-
	Nolletia ciliaris	27	-	-	24	-	42 IVS	-
d)	Schizachyrium sanguineum	73 X	88 X	73	24	-	-	-
	Zornea milneana	-	30	55	29	68	-	-
	Bulbine sp. (not collected)	-	-	-	35	22	42	38
	Sporobolus africanus	-	-	-	24	33	67	38
	Oropetium capense	27	-	-	24	33	100	-
	Sida chrysantha	-	-	46 IVS	24	33	33	-

TABLE 30 Presence percentages of species occurring in at least 20% of the quadrats of Groups 1 and B and none, one, or two other groups of the Bankenveld association analysis (- indicates presence percentage less than 20, see text for explanation of other symbols).

Species	Group						
	1	B	3	4	5	6	7
Andropogon appendiculatus	27	49 X IVS	-	-	-	-	-
Barleria pretoriensis	73	76 IVS	-	-	22	25	-
Chascanum hederaceum	73	79 IVS	100	100 X	-	-	-
Dicoma anomala	91	91	73	29	-	-	-
Diheteropogon amplectens	100 X	100 X	36	-	-	-	-
Eragrostis racemosa	64	91	100	-	-	-	-
Lightfootia denticulata	36	55 IVS	-	-	-	-	31
Polygala rehmannii	46 IVS	21	27	-	-	-	-
Senecio coronatus	27	61 IVS	36	-	-	-	-
Sporobolus pectinatus	46	73 IVS	46	-	-	-	-
Thesium costatum	55	61 IVS	-	24	-	25	-
Trachypogon spicatus	55 X	73 X IVS	64 X	-	-	-	-

Table was drawn up. Six Final Groups, namely 1, 3, 4, 5, 6 and 7, and Group B (consisting of Final Groups 2a, 2b, 2c and 2d) were used for the seven columns of the Table. The presence percentage of every species in each group was computed and all values over 19,9 percent were printed by program CFREQ. Rows of the Table were then formed by the 84 species each of which had a presence of over 39 percent in at least one group. Presence percentages for the species are given in Tables 25 to 30, where species with similar

INSERT TABLES 25 TO 30

distribution patterns through the groups are listed together[14].

Species present in over 40 percent of the quadrats of all seven groups are given in Table 25. In particular, Aristida congesta and Themeda triandra are common throughout the area if a presence of 75 percent is taken as a criterion for within-group abundance.

While all the other species in Table 25 are considered common in all groups, they are slightly less common in one or two groups than in all the remainder. Crabbea angustifolia and Anthospermum rigidum occur in less than half the quadrats of Group 6 and their absence from this Group is significant by Goodall's test. Blepharis integrifolia and Diplachne fusca are also found in less

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(14) In Tables 25 to 30, IVS and -IVS again signify positive and negative significant Indicator values, respectively. X indicates a high cover-abundance rating for the species in most, if not all, quadrats of the group.

than half the quadrats of Group 6. Elionurus argenteus has a fairly low presence percentage in Groups 5 and 6 and Triraphis andropogonoides only occurs in 44 percent of the quadrats of Group 5 and 52 percent of the quadrats of Group B. Apart from the lower presence percentages recorded above, all these species are common in all groups. Species present in over 19 percent of the quadrats of all groups are given in Table 26. Raphionacme burkei has a low presence in Groups 1 and 6. Anthephora pubescens, Dicoma macrocephala, Eragrostis stapfii, Euphorbia inequilatera and Pogonarthria squarrosa do not occur often in quadrats of Group B and have negative Indicator values in the Group. Dicoma macrocephala and Pogonarthria squarrosa are also uncommon in Group 6 and Eragrostis stapfii is uncommon in Groups 3 and 6. Aristida diffusa var. burkei has a high presence percentage in all groups except 4, 5 and 6. Barleria macrostegia and Brachiaria serrata have low presence percentages in Group 6 while Cassia mimosoides and Eragrostis curvula are common in all groups except 5 and 4, respectively.

The 18 species, which have a presence of over 19 percent in all but one group, are listed in Table 27. Chascanum pinnatifidum, Corchorus asplenifolius, Cyperus margaritaceus, Eragrostis superba, Eustachys mutica, Indigofera daleoides, Setaria flabellata and Stipagrostis uniplumis occur in all groups, except B, with presence percentages of over 19. No species are absent from Group 1 only, or only 3, or only 4. Heteropogon contortus has a presence of less than 20 percent in Group 5, while Acalypha sp. (M&E 1267), Chaetacanthus costatus, Helichrysum caespititium, Justicia anagaloides and Kohautia omahekensis have presence percentages of less than 20 in Group 6. Kohautia omahekensis and Justicia anagaloides have negative Indicator values in Groups B and 7, respectively. Bulbostylis burchellii, Cymbopogon excavatus, Ipomoea obscura var. fragilis and Ophrestia oblongata have presences below 20 percent in Group 7.

Sixteen species with presence percentages higher than 19 in five of the seven groups are listed in Table 28. Pygmaeothamnus zeyheri, Rhynchelytrum repens, Senecio venosus, Solanum supinum, Ursinia nana and Cyphocarpa angustifolia occur with presences of over 19 percent in all but Groups 6 and 7. The first three species and the last are also not common in the fourth and fifth groups. Solanum supinum has a high presence (77 percent) in Group 4 only. Ursinia nana occurs in all quadrats of Group 5 and has a positive, significant Indicator value in Group 4. Vernonia oligocephala, Turbina oblongata, Hermannia tomentosa and Cymbopogon plurinodis have presence percentages exceeding 19 in all but Groups B and 3 while Eragrostis tricophora and E. lehmanniana have presences below 20 percent in Groups 1 and 2. Gazania krebsiana, Oxygonum dregeanum, Crassula transvaalensis and Helichrysum cerastioides also have presence percentages below 20 in two groups.

With the exception of species listed in Table 30, all species present in at least 20 percent of the quadrats of only one group, only two groups, only three groups and only four groups are listed in Table 29. Only three species out of the 211 recorded in Bankenveld quadrats, Eragrostis gummiflua, Euphorbia sp. (M&B 70) and Fingerhuthia africana, have presence of over 19 percent in only one group. All three species are confined to Group 6. The first two species have positive, significant Indicator values and F. africana has high cover-abundance estimates in quadrats of the Group. Cynodon dactylon, Diplachne biflora, Mariscus capensis, Tephrosia longipes and Setaria nigrirostris occur with presence of over 19 percent in two groups. Mariscus capensis and Setaria nigrirostris have significant, positive Indicator values in Groups 6 and 4, respectively, while Diplachne biflora and Tephrosia longipes have significant, positive Indicator values in Group B. Elephantorrhiza elephantina, Lippia scaberrima, Menodora africana and Nolletia ciliaris have presence percentages of over 19 in three groups while Schizachyrium sanguineum, Zornea milneana, Bulbine sp., Sporobolus africanus, Oropetium capense and Sida chrysantha have presence percentages of over 19 in four groups. It is observed that in Table 29, presence percentages are generally lower than in Tables 25 and 26. Exceptions in Table 29 are Schizachyrium sanguineum in Groups 1, B and 3 and Sporobolus africanus and Oropetium capense in Group 6.

Presence percentages of species occurring in over 19 percent of the quadrats of Groups 1 and B and none, one, or two other groups are given in Table 30. These species are listed together as it was found that twelve species had roughly the same distribution. Diheteropogon amplectens, Eragrostis racemosa, Polygala rehmannii, Senecio coronatus, Sporobolus pectinatus and Trachypogon spicatus have presences of over 19 percent in Groups 1, B and 3. Lightfootia denticulata has a presence of over 19 percent in Groups 1, B and 7. Barleria pretoriensis. Chascanum hederaceum, Dicoma anomala and Thesium costatum have presence percentages of over 19 in

Groups 1, B and two other groups. Some fairly high presence percentages are found in Table 30. In particular, Diheteropogon amplectens, Chascanum hederaceum, Dicoma anomala, Eragrostis racemosa and Trachypogon spicatus generally have presence percentages of over 65 in the groups in which they occur.

3) Final groups

a) Group 1 (Diheteropogon-Stipagrostis Primary Bankenveld)

Group 1 is defined by the presence of Diheteropogon amplectens and Stipagrostis uniplumis at H.S.$X^2 > 30{,}0$. It is a homogeneous Group, being further subdivided only at the low level of H.S.$X^2 = 7{,}2$. The division on Ipomoea obscura var. fragilis, within Group 1, does not appear to divide the quadrats in an interpretable manner. Considering the low level of the division and the small number of quadrats involved, an important difference between the groups would not be expected. Quadrat 70, classified by the analysis as belonging to this Group does not fit the description given below for the Group. It is therefore omitted from the discussion and is described separately.

Two small patches of quadrats of Group 1 have been mapped (Map 4) north and north-east of Lichtenburg. Other quadrats of this Group occur scattered singly through the north-central and north-western parts of the area.

Nearly all quadrats are located on the crests of small rises, typical of the area, or on waxing slopes from rises. Two quadrats occur in small hollows. Slope is usually so slight as to be unmeasurable. Chert fragments and loose dolomite rocks are usually found on the ground surface in these quadrats. Soil depth varies from 5 to 10 cm. Soil pH is usually 6,5 and occasionally 7,0.

Biotic factors were uniform within the Group. Grazing intensity was light, or moderate, and often the vegetation appeared to have been rested for some time before sampling. Average total basal cover was 14 percent, 6,3 percent being contributed by the tall grass stratum (60 to 90 cm tall with many 75 cm tall) and 7,6 percent by the short grass stratum (about 16 cm tall but ranging from 5 to 35 cm tall). The mean number of species per quadrat was 49,5 with a standard deviation of 3,4. The maximum number of species in a quadrat was 54 and the minimum was 43. Quadrats of this Group are thus rich in species, containing the highest average number of species of any Bankenveld group studied. The low standard deviation indicates that quadrats are all equally rich. Species present in over 19,9 percent of the quadrats of Group 1 are given in Tables 25 to 30.

This small Group represents Bankenveld on relatively deep, dolomite-derived soils that have been rested in the recent past or have at least been protected from mismanagement. All quadrats are also not found near the diamond diggings, a source of past disturbance. The Group is thus referred to as Primary Bankenveld. The Group is named after the two species positively defining it in the hierarchy, Diheteropogon amplectens and Stipagrostis uniplumis. These species also had high cover-abundance ratings in most quadrats of the Group.

Quadrat 70, while occurring in the same landscape as the other quadrats of the Group, differs by being very heavily grazed and its vegetation being in poor condition. Soil is very shallow and large sheets of rock are exposed in the quadrat. On these grounds it is excluded from the description of Group 1.

b) Group 2 (Diheteropogon-Schizachyrium Bankenveld)

Group 2 is defined by the presence of Diheteropogon amplectens and the absence of Stipagrostis uniplumis. It is further subdivided at H.S.X^2 = 13,1 on the presence or absence of Sporobolus pectinatus. The three quadrats, which form Group 2a, are split off the +S. pectinatus leg at H.S.X^2 = 8,5. A large amount of residual group heterogeneity is apparently removed by this division as the next division is at a higher H.S.X^2 value. Groups 2b and 2c are formed by division on Heteropogon contortus at H.S.X^2 = 10,4. Group 2d is formed by quadrats in the -S. pectinatus leg of Group 2. As a whole, Group 2 appears homogeneous, being retained as an entity from H.S.X^2 = 30,0 to 13,1. At a level of H.S.X^2 = 8,5, however, the 33 quadrats of this Group are divided into four groups. The largest Final Group, 2b, contains 14 quadrats, Groups 2d and 2c contain 10 and 6 quadrats, respectively, and Group 2a contains only three quadrats. Group 2 will be described as a whole and peculiarities of each Final Group will be mentioned.

Quadrats of this Group form a belt from east to west across the study area. Group 2b is concentrated in the eastern and central parts of the belt. Group 2a is restricted to three quadrats in the south-western corner and quadrats of Group 2c occur among those of Group 2b. Quadrats of Group 2d are found at the western end of the belt and along the south-central edge of the belt. Only three quadrats of Group 2 fall outside the area mapped as such. In comparison with some other groups, whose quadrats are scattered through the study area, this is a 'neat' Group. Provisionally, the distribution of this Group has been extended to include areas not classified as belonging to any other group and areas that were not sampled. A reason for doing so is given later.

Over two thirds of the quadrats of Group 2 occur on crests of rises or on very gentle waxing south- and north-facing slopes. The other third, which are found scattered through all four Final Groups, are in very shallow depressions, on waning slopes to drainage lines, or in small sand-filled sinkholes.

Soil is usually 5 to 8 cm deep with chert gravel littered on the soil surface. A solid sheet of dolomite is not found in any quadrat. Soil pH varies between 6,5 and 7,0 and no soil HCl reaction is recorded.

With five exceptions all quadrats were lightly grazed or rested and the vegetation was in good condition. Some of the samples were from inside fenced maize lands on soil too shallow for ploughing. Vegetation in these situations was protected from grazing, except after the maize harvest, when cattle are usually allowed to eat the dry maize stalks. The exceptional quadrats were heavily grazed and trampled and sheets of dolomite were often exposed in them. These quadrats are not excluded from the calculations on which the species lists given below are based, because some, if not all of them, could have been heavily grazed for too few years for their species composition to have altered. Under these circumstances, the quadrats will be correctly classified as the classification is based on the floristic composition of the quadrats when sampled.

Average total basal cover in Group 2 was 5,0 percent for the tall grass stratum (usually 75 cm but ranging from 60 to 90 cm in height) and 5,7 percent for the short grass stratum (usually in the range 15 to 30 cm tall). The averages for Group 2b were slightly greater than the overall averages and those for Groups 2a, 2c and 2d were equal to, or slightly less than, the averages for Group 2 as a whole. The mean number of species in each quadrat of this Group was 43,6 (SD = 5,8). Species present in over 19,9 percent of the quadrats of Group 2 are given in Tables 25 to 30.

Groups 2a and 2c are too small to yield reliable presence percentages and are not discussed further. With the exception of dividing species, no species could be found restricted to either Groups 2b or 2d.

On the grounds of the species common to the subgroups and the similar habitat and management features of the quadrats of Group 2 it was decided not to subdivide the Group for mapping purposes. Diheteropogon-Schizachyrium Bankenveld is the most widespread Group in the analysis. It is considered to be the 'normal' or 'typical' Bankenveld of the study area. In distribution, Diheteropogon-Stipagrostis Primary Bankenveld (Group 1) forms an extension of this Group and represents a higher successional stage (less disturbance) in the Bankenveld Land System with a slightly different habitat.

Group 2 is named after a positive dividing species, Diheteropogon amplectens, and Schizachyrium sanguineum, a species with a presence of 88 percent in the Group. Both species have high cover-abundance estimates in most quadrats of the Group.

c) Group 3 (Chascanum-Eragrostis racemosa Sandy Bankenveld) and Group 4 (Chascanum-Anthephora pubescens Sandy Bankenveld)

These two Groups are discussed together as they are split at the low H.S.X^2 level of 18,1. The homogeneity of each Group is indicated by neither's being further subdivided until H.S.X^2 $\angle$9,5. The combined Group, 3 and 4, is also homogeneous, being maintained as a Group from H.S.X^2 = 38,6 to H.S.X^2 = 18,1. Thus, as a combined Group and as separate entities, Groups 3 and 4 are relatively homogeneous. The combined Group is defined by the absence of Diheteropogon amplectens and the presence of Chascanum hederaceum. Group 3 is defined by the presence of Eragrostis racemosa and Group 4 by the absence of this species.

Quadrats belonging to both Groups occur along the western boundary of the area, in a round patch in the north-west, and the few other samples occur scattered through the remainder of the sampled area. Distribution of the two Groups cannot be separated. Group 4 is the larger of the two and the usual pattern is for a quadrat of Group 3 to occur among a cluster of Group 4 quadrats.

Groups 3 and 4 form a clear ecological nodum associated with a thin, sandy overburden to dolomite. In the majority of quadrats, soil is shallow (5 - 10 cm), but is occasionally over one metre deep. In most quadrats, the soil surface is free of rock, or contains only scattered, small, chert fragments. It is possible that aeolian sand of Kalahari origin has blown from the west onto the edge of the area, forming a thin veneer over dolomite. Such a movement of sand would be in agreement with the views of Harmse (1967), illustrated in Fig. 3. Within the study area, wind-blown sand has collected in sink-holes and other depressions to form a similar habitat. In Group 4, four quadrats are located in local depressions while a number of quadrats from both Groups occur on flat plains or crests of rises on which sand could easily accumulate. A remarkable feature is, however, that over half the quadrats in Group 3 and over a third of the quadrats in both Groups occur on slightly sloping ground where it would be expected that erosion of sand would be greatest and accumulation least. As the rainfall is relatively low and run-off in the dolomite minimal, sand deposited on a slope is, however, not transported easily. Soil pH is about 6,5 in both Groups.

Moderate to moderate-heavy grazing was found in most quadrats of both Groups. When light grazing was recorded, another disturbance factor, like proximity to diamond diggings, was usually noted.

Mean number of species per quadrat in Groups 3 and 4 were 46,6 (SD = 8,2) and 41,0 (SD = 7,1), respectively. The maximum numbers of species were 51 and 56, respectively, and the minimum numbers were 23 and 31, respectively. The tall grass stratum was 60 to 75 cm high in both Groups, with a maximum of 90 cm in Group 3. The short grass stratum was 10 to 30 cm high in Group 3 and 10 to 20 cm high in Group 4. Total basal cover of both Groups was low. Basal cover of the tall grass stratum in both Groups averaged about 3 percent and of short grasses 6 percent. Total basal cover was slightly lower in Group 4 than in Group 3.

Species present in over 19,9 percent of the quadrats of Groups 3 and 4 are given in Tables 25 to 30. Many species are common to both Groups and about eight species are found particularly in one or other of the two Groups.

Similar names are given to these two Groups as they are rather similar in both floristics and habitat. Both are named after the dividing species positively defining them:- Chascanum hederaceum. Anthephora pubescens, used as a second name for Group 4, often scored a high cover-abundance estimate in quadrats of the Group and has a high presence percentage in the Group.

d) Group 5 (Corchorus-Ursinia Bankenveld of Disturbed Sites)

Quadrats of this small Group are scattered through the study area. The two areas mapped as being of this Group were delimited more on the writer's knowledge of the area than on the distribution of quadrats of the Group. In fact, the area mapped as such in the south-east does not contain a single quadrat of this Group. Group 5 is defined by the absence of Diheteropogon amplectens and Chascanum hederaceum and the presence of Ursinia nana. The marked floristic composition which is a result of the secondary nature of the vegetation brings these quadrats together on the hierarchy. Some of the quadrats are laid out near diamond diggings, others on abandoned lands and the rest on heavily trampled and overgrazed vegetation.

All physiographic combinations are represented. Some quadrats are on crest of rises, some in hollows and some in intermediate positions. North-facing and south-facing aspects, as well as level sites, are represented. Soils are usually shallow, being, in general, from two to eight cm deep and often being gravelly where occurring in fossil river courses. Deeper soil is found occasionally, the deepest for this Group being recorded as 0,5 m.

Mean number of species per quadrat was 40,0 (SD = 7,1) with the maximum being 56 and the minimum 31. Total basal cover averaged 10,6 percent, only 2,8 percent of which was accounted for by the tall grass stratum (usually 60 cm tall but occasionally 90 cm tall). The low total cover and large percentage thereof accounted for by the short grass stratum (15 to 25 cm high) is a further indication of the disturbed nature of the vegetation.

Species present in over 19,9 percent of the quadrats of Group 5 are given in Tables 25 to 30. As Corchorus asplenifolius and Ursinia nana are the only two species which occur in every quadrat, the Group is named after them. Although it has a high presence percentage in Group 4 as well, Ursinia nana is the dividing species defining this Group. Corchorus asplenifolius is fairly common throughout the entire area but does not have a presence of 100 percent in any other Group.

Group 5 represents areas of disturbed vegetation within the study area. Thus, the areas next to abandoned diamond diggings are mapped as belonging to this Group, even though few quadrats were located there. The influence on the vegetation surrounding the diggings of over 100 000 people (Williams 1930) who flocked to the diamond fields from 1926 to 1929 must have been tremendous and it is unlikely that the vegetation has fully recovered yet. Other types of disturbed vegetation are also included in this Group but as the areas are usually small they are not mapped.

e) Group 6 (Fingerhuthia-Oropetium Bankenveld of Dolomite Sheets)

With the exception of three quadrats, which occur scattered through the study area, the quadrats of this Group occur to the immediate north of Lichtenburg, in the southern-most part of the Bankenveld Land System.

Quadrats of this Group are found on shallow soils where solid dolomite sheets are exposed on the surface. Soil, if it is present, is usually only 2 to 5 cm deep. Soil pH is usually 7,0 to 7,5, in other words slightly more alkaline than in most other groups. In three quadrats a slight soil HCl reaction was recorded.

Quadrats of this Group occur on extensive plains, in slight hollows and on gentle slopes near crests of plains.

Grazing in seven quadrats was light and the vegetation appeared undisturbed. In the other five quadrats of the Group, however, grazing was moderately-heavy to heavy. Average total basal cover was just under 10 percent, with approximately equal contributions from the tall (usually 75 cm, but ranging from 60 to 120 cm in height) and short (either 10 to 15 cm or 30 to 45 cm tall) grass strata. The mean number of species per quadrat was low (36,5) but the standard deviation of the mean was high (SD = 7,4), indicating that while some quadrats were very poor in species, others were rich. The lowest number of species recorded from a quadrat of this Group was 19 and the highest was 49.

Species present in over 19,9 percent of the quadrats of Group 6 are given in Tables 25 to 30. Eragrostis gummiflua, Euphorbia sp. (M&B 70) and Fingerhuthia africana have presence percentages of over 19,9 in Group 6 only (Table 29).

The Group is named after Oropetium capense, a diminutive grass found in every quadrat of this Group but in few other quadrats (Table 29) and Fingerhuthia africana, which often has a high cover-abundance rating in quadrats of this Group and does not have a presence greater than 19,9 percent in any other Group. Gaff (1971) reported that O. capense could withstand virtually complete desiccation, a necessary prerequisite for survival on rock sheets with little soil as found in quadrats of this Group (see Chapter 6 for further discussion).

f) Group 7

Group 7 is the last Group of the hierarchy and is defined by the absence of four dividing species, namely Diheteropogon amplectens, Chascanum hederaceum, Ursinia nana and Oropetium capense. The Group defined in this way usually contains all the quadrats which cannot be included in any other group and is rather heterogeneous.

Quadrats of this Grou) do not form a mappable unit, being scattered diffusely across the northern and southern boundaries of the area from east to west. This Group is neither mapped nor named as it is considered a collection of quadrats which should have been included in other Groups but which, by chance, lacked the necessary defining species. Re-allocation of these quadrats was not considered worthwhile.

More than half the quadrats are on slight, south-facing slopes and most of the rest are on level ground. All sites in the geomorphic cycle from hollows to crests of rises are represented.

Grazing was light and the vegetation had been rested in about half the quadrats, one quarter had been moderately grazed and the remainder had been heavily grazed and disturbed before sampling. Basal cover of the short grass stratum (10 to 15 cm tall) was six percent and basal cover of the tall grass stratum (75 cm, but ranging from 60 to 90 cm) was seven percent. The mean number of species per quadrat was 32,9 with a standard deviation of 5,6. The minimum number of species recorded in a quadrat of the Group was 24 and the maximum was 43.

Soil is shallow, usually from five to 15 cm deep but may be over one metre deep or, as in some quadrats, be very shallow with sheets of dolomite exposed. Soil pH varies between 6,5 and 7,0 and no soil HCl reaction was recorded.

Species which occur in over 19,9 percent of the quadrats of this Group are listed in Tables 25 to 30.

DISCUSSION AND CONCLUSIONS

Sampling strategy

It is well documented that strictly systematic and random sampling, although deemed statistically justifiable and even preferable, are inefficient (Taylor 1969, Werger 1973). This is chiefly because such strategies result in the inclusion of narrow ecotones in collections of samples, which are then heterogeneous (Grunow 1965a, Lambert 1972). It also leads to undersampling generally-recognised but small vegetation units, such as vleis (marshes) and dolerite dyke communities, and over-sampling of large units. Small vegetation units might then not be identified by a statistical method, such as association analysis, which is programmed to terminate at a certain minimum number of samples. Even a group of only one or two samples will, of course, be identified by association analysis if its constituent quadrats are sufficiently similar to each other.

In a vegetation survey such as the present one, more interest is vested in dominant vegetation communities than in narrow ecotones and vegetation units of small area, while areas of intermediate size should be adequately sampled to enable identification and characterisation by the statistical process used. The stratified sampling strategy used for this study ensured that a representative sample of the variation was obtained (see also Werger 1973), while the random element ensured that the sampling was statistically acceptable. Such a strategy is of particular importance where the number of samples is strictly limited, as it was in this study.

It is well documented that sample shape influences the number of species recorded in a sample. Long, narrow samples generally yield more species than circular or square ones (Greig-Smith 1964, Shimwell 1971). While square samples (16 m^2) were used for the association analyses described in this Chapter, triangular samples were used for some technique studies described later. It was assumed in this study that the differences in shape between triangles and squares would have little influence on the number of species recorded and that observed differences in number of species would be dependent mainly on differences in sample area.

In long, narrow samples the perimeter is longer than in square or circular samples with the same surface area. Therefore, more plants straddle the boundary line and proportionally more decisions as to whether plants are inside or outside the sample are needed on long, narrow samples. Although the perimeter is longer in relation to surface area in a triangle than in a square, it was close enough as not to cause marked sampling differences from this cause.

It is preferable to establish optimum sample size in the study area instead of using a size derived elsewhere (Lambert 1972). In this study, it was considered that compatibility between studies was of greater importance than the derivation of a unique size for this project. Furthermore, results of pilot studies showed that a slightly smaller sample (12 m^2) would have been adequate and 16 m^2 was considered large enough to be a 'safe' minimum size for the entire Highveld Ecological Survey (J.C. Scheepers[1]: pers. comm.).

Extensive cultivation in the CT Grassland Land System made sampling difficult. Not only are clusters of samples situated far apart, but great difficulty was experienced in getting samples representative of all vegetation types which were presumed to have existed in the area previously. Some types have almost certainly disappeared completely. As it is vegetation on soils that are less suitable for cultivation which remains, a marked sampling bias towards vegetation on these soils and away from that on soil suitable for cultivation is likely to have taken place.

The number of samples in both Land Systems is small. In CT Grassland there was the physical problem of fitting samples into a restricted area of natural vegetation while in Bankenveld it was considered that the major vegetation types had been adequately sampled by 110 samples. The limited period for field-work during the present study also affected the number of samples which could be taken.

There were two reasons for the small number of habitat variables recorded at each site. Firstly, as the study was conceived as a semi-detailed survey of short duration, intensive study of ecological interrelationships was not planned. Secondly, the number of habitat factors which can be studied in Bankenveld is limited by the nature of the soil. In most places, sheets of dolomite are exposed at the surface and the plants are rooted between rocks. Measurement of field capacity, wilting point, or similar measures are therefore unrewarding.

Methodological aspects

The broad differences between Bankenveld and CT Grassland Land Systems, outlined in Chapter 2, are shown to be supported by quantitative analysis of the vegetation. The Total association analysis separated most quadrats laid out in Bankenveld from those laid out in CT Grassland. Nineteen Bankenveld quadrats occurred in groups consisting mainly of CT Grassland quadrats but Bankenveld groups never included CT Grassland quadrats. It was therefore concluded that certain Bankenveld vegetation quadrats resembled vegetation of CT Grassland groups in their floristic composition, but that no CT Grassland samples resembled Bankenveld groups. Of Bankenveld quadrats classified with CT Grassland groups, 42 percent were from Group 7 of the Bankenveld hierarchy and 37 percent were from Group 6 of the same classification. Group 7, the last group of the Bankenveld classification, was found to be a heterogeneous group of quadrats. The species composition of many Group 7 quadrats could be such that, by chance, they did not contain the dividing species necessary to include them in a group in which they would be appropriate. In the Total analysis also, these quadrats were shown to be a heterogeneous collection by their being scattered through a number of final groups.

Apart from strong, positive species association within quadrats of each Land System and negative associations between them, floristic richness may be partly responsible for the major automatic division between Bankenveld and CT Grassland. A floristically-rich group of quadrats is defined as one with a relatively high mean number of species within each quadrat of the group and a floristically-poor group is the opposite. That floristic richness of quadrats may influence the nature of the resulting hierarchy was noticed on inspection of the mean numbers of species per quadrat in each final group of both hierarchies. In the Bankenveld classification, the mean decreases steadily from Group 1 (49,5) and Group 2 (43,6) to Groups 6 (36,5) and 7 (32,9), across the hierarchy from left to right. Thus, floristically-rich groups split off first and floristically-poor quadrats generally remain until last. Although evidence is not available, it is conceivable that more positive species associations are present in floristically-rich collections of quadrats, making the collections more homogeneous and therefore more likely to be split off.

A similar decrease from left to right in mean number of species per quadrat was found in the Total analysis. The overall mean number of species per quadrat is, however, much lower. The overall average in the 110 Bankenveld quadrats exceeds 40. In CT Grassland Groups 4b, 5b, 6 and 7a, which contain most species per quadrat, the mean is less than 27. The average decreases steadily to the last Group, 9c, with a mean of 15,2. Thus, if floristic richness is a factor controlling the results of the classification, the marked division between

Bankenveld and CT Grassland Land Systems would be expected. It is also the possible explanation for floristically-poor Bankenveld quadrats of Groups 6 and 7 occurring with floristically-poor CT Grassland groups in the Total analysis.

Austin (1972) has pointed out that association analysis is sensitive to rare species on account of the way in which associations (X^2) are calculated. In order to further study the influence of floristic richness on association analysis, a factor not mentioned by Austin (1972), analyses were undertaken where the number of species per quadrat remained constant throughout. Results are given later.

To obtain the greatest amount of information from the association analyses they had to be interpreted at more than one stopping level. A single stopping rule, as initially proposed by Williams & Lambert (1959, 1960), was not adequate. It is considered, furthermore, that experience with use of the method greatly improves the result that is obtained. Association analysis should be considered as an aid in the study of vegetation and not as a tool to be applied by technicians with no training in its use and misuse.

Although a few quadrats could not be successfully re-allocated, the use of species recorded around the edge of the quadrat to re-allocate quadrats was successful. Had total floristic composition also been taken into account in the re-allocation procedure and not only habitat features and species in the surrounds of quadrats, an even more successful re-allocation may have been realized.

Program CFREQ was most useful for summarising presence percentages for each species of each group as well as for calculating the mean number of species per quadrat. Indicator values, also calculated by this program, were of use for determining significance levels for species occurring more commonly inside a group than outside it. Used in conjunction with positive and negative dividing species and cover-abundance estimates, Indicator values enabled good floristic definitions of groups to be made. On the other hand, negative Indicator values, given to species occurring more frequently outside a group than inside it, were of limited use. As only species with presence percentages of over 19,9 were printed by CFREQ, many species with negative Indicator values were obviously omitted. Positive and negative Importance values were therefore imbalanced.

Although no objective criteria for measuring success are known, it may be concluded that the technique of association analysis performed adequately in providing a generally-interpretable classification of the vegetation. It is shown later that differences of varying importance are brought about by altering either the classification strategy or the size of the mask used to exclude rare species. A perfect classification of a data set of this size probably does not exist and the utility of a particular strategy as an aid for the study of the vegetation should be the criterion on which the classification is judged.

Similarities between pairs of Total analysis groups

1) Similarities between Groups 4b and 6

In discussing Group 6, the similarity between Group 4b (Short Stipagrostis uniplumis Calcareous Grassland) and 6 (Tall Stipagrostis uniplumis Calcareous Grassland) was mentioned. In addition to the similarity of dividing species, these Groups share the same geological substrate, geomorphology and soils. Soils are, however, slightly deeper in Group 6 and HCl reaction is only slight, or absent, in contrast with the strong or moderately strong reaction in Group 4b. Mean basal cover of the tall grass stratum in Group 6 was double that in Group 4b. The mean number of species per quadrat was the same in both Groups. Three species, Stipagrostis uniplumis, Fingerhuthia africana and Convolvulus ocellatus var. ornatus were very common in these two Groups but nowhere else.

Where still uncultivated, the vegetation of Groups 4b and 6 has been mapped as one unit, Stipagrostis uniplumis Calcareous Grassland. Inspection in the field will enable classification into the tall or short form to be made on the basis of the above comparison. It is not possible to separate them on aerial photographs.

Most of the area formerly occupied by S. uniplumis Calcareous Grassland has been ploughed for maize cultivation. Most of the rest, where the soil is too shallow for ploughing, has been excavated to supply limestone for local cement factories or has, at least, been bought for this use in future. The area covered by S. uniplumis Calcareous Grassland is decreasing rapidly as a result of this activity.

2) Similarities between Groups 5b and 8

Groups 5b (Elionurus argenteus Secondary Grassland) and 8 (Elionurus argenteus Primary Grassland) have a number of features in common and, in fact, the reason for the association analysis split is not clear. Most quadrats of both Groups are found on rocks of the Ventersdorp system, on flat plains where the soil series is Soetmelksvlei. In Group 5b, half the quadrats are on shallow soil (mean depth 15 cm), while the other half are on deeper soil (over 80 cm) while in Group 8, soils are usually over 60 cm deep. Soil pH and HCl reaction are similar in the two Groups.

In Group 5b, quadrats on the deeper soils are heavily grazed while quadrats on the shallower soils are rested or only lightly grazed. In Group 8, where the soil is generally deep, grazing is light or the vegetation has been rested. One of the main differences is, thus, a disturbance factor of grazing pressure interacting with the occurrence of shallow soil, resulting in the names 'primary' and 'secondary' for these Elionurus argenteus Grasslands.

Basal cover of the tall grass stratum was slightly higher in Group 8 than in Group 5b but cover of the short grass stratum was the same. A slightly greater number of species occurred in quadrats of Group 5b than in those of Group 8.

Hibiscus microcarpus was the only species which occurred commonly in these two Groups and nowhere else.

Species which occurred in over 60 percent of the quadrats of both Groups 5b and 8 include:-

Anthospermum rigidum
Aristida congesta
Barleria macrostegia
Elionurus argenteus
Eragrostis curvula
Heteropogon contortus
Setaria flabellata
Themeda triandra
Triraphis andropogonoides

Species which are common in Group 5b (in over 60 percent of the quadrats) but are either rare in, or do not occur in Group 8 (less than 60 percent of the quadrats) include Brachiaria serrata (the dividing species between the two groups), Aristida diffusa var. burkei, Crabbea angustifolia and Justicia anagaloides. Eustachys mutica is the only species found in over 60 percent of the quadrats of Group 8 and in fewer than 40 percent of the quadrats of Group 5b.

As these two Groups are similar, except for management and soil depth factors, they are mapped as one unit. As quadrats of both Groups are usually intermingled, the Groups would be difficult to map separately.

3) Similarities between Groups 7a and 9aii

There are many similarities between Group 7a (Cymbopogon plurinodis Grassland) and Group 9aii (Secondary Cymbopogon plurinodis Grassland), and they are mapped together. Group 9aii is, however, too small for a detailed ecological analysis and interpretation. The two Groups have geological, geomorphological and soil characteristics in common. Soils are slightly shallower in Group 9aii than in Group 7a. Biotic influences were variable in Group 7a but grazing was heavy and trampling marked in Group 9aii. Mean basal cover and number of species per quadrat were lower in the latter Group.

Cynodon dactylon, Eragrostis curvula, Eustachys mutica and Triraphis andropogonoides occur more commonly in Group 9aii than in Group 7a. As the first two of these species are associated with disturbed habitats and as grazing and trampling are generally more severe in 9aii than in 7a, the latter Group is called Secondary Cymbopogon plurinodis Grassland and the former, Cymbopogon plurinodis Grassland.

General vegetational aspects

In the Total association analysis, division between Bankenveld and CT Grassland quadrats is fairly clear. As the Bankenveld area was considered most important from a vegetational point of view and as there was some mixture of Bankenveld quadrats in groups of predominantly CT Grassland quadrats, a separate analysis of the 110 Bankenveld Land System quadrats was undertaken. It was not considered profitable to interpret Bankenveld final groups in both the Total analysis and the Bankenveld analysis, particularly as other classifications of Bankenveld data are interpreted later. In a general way, results of the Bankenveld analysis and Bankenveld part of the Total analysis are similar.

In CT Grassland, eleven final groups are recognised and described and six vegetation types are mapped. Two final groups, Short and Tall Stipagrostis uniplumis Calcareous Grassland, occur on soils overlying surface limestone deposits with the same geomorphology and soil series. Soils are generally slightly deeper and basal cover of tall grasses is double in quadrats classified as Tall Grassland in comparison with quadrats of Short Grassland. In both Groups grazing is usually light. As these two Groups could not be separated on aerial photographs they are mapped as one unit; Stipagrostis uniplumis Calcareous Grassland. The community is found around Lichtenburg and in a belt extending west of the town.

Another two final groups, Elionurus argenteus Secondary Grassland and E. argenteus Primary Grassland occur on rocks of the Ventersdorp system. Heavy grazing and soil erosion are often recorded from quadrats of the former while the vegetation is usually in good condition in the latter Group. These two Groups are also mapped as one unit: Elionurus argenteus Grassland. Most Elionurus argenteus Grassland is found south-west of Lichtenburg.

Two final groups also occur on Dwyka tillite substrate. They are Cymbopogon plurinodis Grassland and Secondary Cymbopogon plurinodis Grassland. Difference between these two Groups are also in degree of biotic influence but, as there are only three quadrats in the latter Group, the distinction does not carry much weight.

Three final groups, Acacia karroo Savanna, Acacia karroo

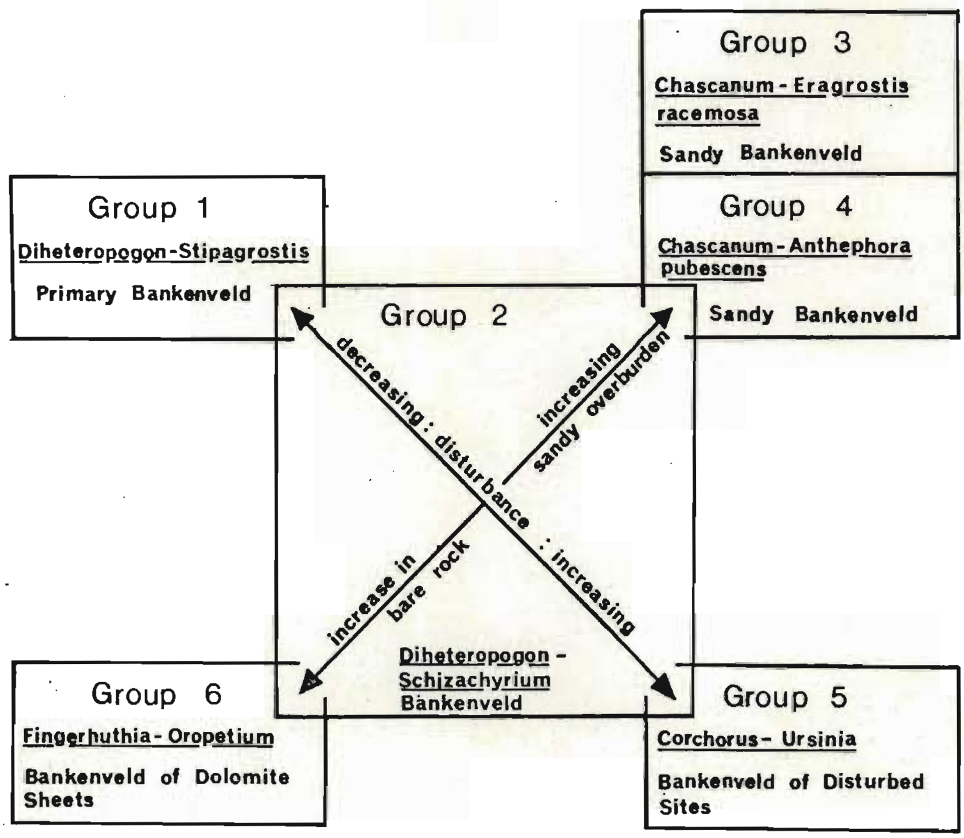

Fig. 9 Suggested relationships between Bankenveld association analysis groups.

Open Woodland and Drainage Basin Acacia karroo Open Woodland are found on the medium- and poorly-drained soils of the area. Heavy grazing and trampling are usual in quadrats of these Groups. Most quadrats are situated on Ventersdorp Series rocks. In all three Groups a woody element is present with Acacia karroo as the dominant tree and shrub species. The three Groups are mapped separately. The unsampled Harts River valley is provisionally mapped as Drainage Basin A. karroo Open Woodland.

Two final Groups, 7a and 7b, are neither named nor mapped. It is found that they are not homogeneous and that their component quadrats occur scattered through the study area.

It is concluded from the description given that the major vegetational differences in the CT Grassland Land System can be related to the geological substrate and gross soil characteristics. Within major groups, management is often an important factor although, in some cases, there are not enough quadrats in a group for even a reasonable degree of certainty. Two final groups, one of only three quadrats, from adjacent legs of the hierarchy could not be interpreted.

In the Bankenveld association analysis ten final groups are distinguished. For discussion and mapping the four final groups of Group 2 are lumped and for mapping purposes Groups 3 and 4 are also lumped. Suggested relationships between Bankenveld groups are indicated in Fig. 9, which should be borne in

INSERT FIG. 9

mind in the following discussion.

It is considered that Group 2 (Diheteropogon-Schizachyrium Bankenveld) is the typical vegetation of the Bankenveld Land System. Group 1 (Diheteropogon-Stipagrostis Primary Bankenveld) consists of quadrats laid out in vegetation that had been well managed. Group 1 is closely related to Group 2 but has experienced less selective or heavy grazing and trampling in the past. It may be considered as the 'climax' vegetation type, although possibly occurring in a slightly different habitat.

Quadrats of Groups 3 and 4 (Chascanum-Eragrostis racemosa Sandy Bankenveld and Chascanum-Anthephora pubescens Sandy Bankenveld) occur together on the western edge of the Bankenveld Land System and in a circular patch in the north-west of the study area. Differences between the two Groups are not clear. Both are found where sand overlies dolomite. It is suggested that aeolian sand has been blown from the west over the dolomite and provided the habitat for these Groups.

Past disturbance in the area was discussed in Chapter 2. It is suggested that quadrats of Group 5 (Corchorus-Ursinia Bankenveld of Disturbed Sites) are those in vegetation which has been disturbed in the past.

Exposed sheets of dolomite are characteristic of parts of Bankenveld, particularly in the area to the immediate north of Lichtenburg. Group 6 (Fingerhuthia-Oropetium Bankenveld of Dolomite Sheets) is the vegetation typical of such areas.

Group 7, the last group of the Bankenveld hierarchy was neither named nor mapped. In general, it was found that Bankenveld was homogeneous and that the chance absence of a species could easily misclassify the quadrat. It is not surprising therefore, that one group was not interpretable.

Within the whole study area and out of two association analyses, 11 groups are mapped out of 21 final groups. Fifteen groups, one consisting of four sub-groups, are interpreted. Although sample size may contribute to the apparent misclassification of quadrats of these groups, the small total number of samples is a more likely reason.

CHAPTER 4

CLASSIFICATION OF BANKENVELD BY NEWER AUTOMATIC METHODS

INTRODUCTION

Goodall (1953a) proposed the first method for automatic classification[15] of vegetation samples, being closely followed by Williams & Lance (1958), Williams & Lambert (1959, 1960) and Lance & Williams (1965) with the next method; association analysis. Shortly after that, inverse analysis (Williams & Lambert 1961a) and nodal analysis (Williams & Lambert 1961b, Lambert & Williams 1962) were described. More sophisticated techniques, including information analysis (Lance & Williams 1968), dissimilarity analysis (Macnaughton-Smith et al. 1964), agglomerative

(15) The term, automatic classification, is preferred to objective (or non-subjective) classification (see Miller 1966, Grunow 1965a and Lambert 1972), as the former term describes the process more adequately and it does not imply that it is superior to other methods of vegetation classification or that other methods are more subjective.

clustering (Orloci 1967) and less computationally demanding techniques such as group analysis (Crawford & Wishart 1967), followed rapidly as the need for and utility of automatic classification techniques were realized. Many of the techniques are reviewed by Williams (1971).

The main distinctions between the various techniques of hierarchical classification lie between agglomerative and divisive strategies on the one hand and between monothetic and polythetic models on the other. Agglomerative and divisive strategies are concerned with the actual construction of the hierarchy (see Phipps 1971) while monothetic and polythetic models are concerned with the number of attributes used directly in the definition of classes (Lambert & Dale 1964). In the following discussion, the 'top' of the hierarchy always refers to the starting point of a divisive strategy and to the end point of an agglomerative strategy while the 'bottom' refers to the opposite end of the hierarchy.

Classification of samples is divisive when the whole population is divided into successively smaller groups, each group being examined independently for possible further subdivisions. It is agglomerative when classification starts with the individual samples, the most similar samples being successively merged to form synthetic 'samples' until all individuals are united in a compound 'sample'. Divisive strategies start with maximum information about the entire population so that most distortion is expected at the bottoms of the hierarchies, where final divisions are made. Agglomerative strategies start with many, single samples of minimal information and most distortion is expected at the tops of the hierarchies where final fusions are made. Whether most distortion is at the top or the bottom of a hierarchy is important as one is often interested only in the topmost divisions of the hierarchy and it is required that these divisions, or fusions, be as free from distortion as possible. In terms of freedom from distortion, therefore, divisive strategies are superior to agglomerative ones. A further, cost advantage of divisive strategies is that, in them, classification may be terminated at any desired level, thus saving computer time, while agglomerative strategies must be completed to obtain the topmost fusions even though the bottom of the hierarchy may be ignored later. As there are these good reasons for preferring divisive strategies to agglomerative ones, use of two divisive strategies in this Chapter is justified.

Polythetic models employ a combination of characters to specify either a division or fusion while only one character is used by monothetic models. Both monothetic and polythetic models have their advantages and disadvantages. Key dividing species, which may be useful in the field, are obtained from monothetic models only (see Grunow & Lance 1969). On theoretical grounds, however, polythetic models are less subject to distortion, are stable and are, by their nature, more informative (Williams, Lambert & Lance 1966, Lambert 1972). Monothetic models have the advantage of being generally computationally faster. Every group at every stage (except the entire population) of a monothetic classification is defined by the presence, or absence, of specified attributes while the groups of polythetic classifications are defined by their general overall attribute similarity. Williams, Lambert & Lance (1966) pointed out that, at that time, agglomerative-polythetic models, like agglomerative information analysis, were the most common methods of automatic classification. They considered divisive-polythetic models, of which AXOR (see later) is an example, to be computationally difficult and not sufficiently developed. Association analysis and divisive information analysis are examples of divisive-monothetic models.

With few exceptions, all past South African applications of automatic classification techniques have used only association analysis and, occasionally, its counterpart, inverse analysis (for example by Grunow & Lance 1966). The main reason for newer models not having been applied is that while computer programs for association analysis have been available in South Africa, programs for other techniques have not. The three association analysis programs used in South Africa, WB11, ASOC and AANAL, will be briefly reviewed below for the historical record. All three are based on association analysis as described by Williams & Lambert (1959).

WB11 was written in FORTRAN II by M.C Pistorius[16] in collaboration with J.O. Grunow[9] and used first on an IBM 704

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(16) Address: Mrs M.C. Pistorius, then of the National Research Institute for Mathematical Sciences of the Council for Scientific and Industrial Research (C.S.I.R.), P.O. Box 395, Pretoria.

computer and later on an IBM 360 computer at the Council for Scientific and Industrial Research (C.S.I.R.). The program was used by Grunow (1965a) and other early automatic vegetation classifiers including Roberts (1966), Miller (1966), Downing (1966) and Miller & Booysen (1968). The most recent users were probably Woods & Moll (1967). Use was limited by the relatively high cost of computer-time at the C.S.I.R. The second program, ASOC, was written in PLAN by H.H. von Broembsen[17] for an ICL computer. This program was used by Scheepers (1969) for classification of the vegetation of the Kroonstad Key Area of the Highveld Ecological Survey. Use of ASOC was hindered because ICL computers were not easily accessible to the Botanical Research Institute. The third program, AANAL, was written by the author in FORTRAN IV and has been used on IBM 1130 and Burroughs B6500 computers. It is the only known association analysis program currently used in South Africa. It was used for all the association analyses described here.

In this Chapter, procedures for a polythetic-divisive model, called AXOR (AXis ORdination), and a monothetic-divisive model, known as divisive information analysis (DIVINF), are described. Results of their application to Bankenveld data are given and

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(17) The late Mr H.H. von Broembsen, Botanical Research Institute, Private Bag X101, Pretoria.

these results are briefly compared with the Bankenveld association analysis results of Chapter 3. The first, brief account of AXOR is by Lambert (1972) and a slightly longer description is given by Lambert et al. (1973). As a detailed step-by-step account has not yet been published and as the technique has not been previously applied to South African data a detailed description (after S.E. Meacock[18]) is given below. As DIVINF has already been used in South Africa (Grunow & Lance 1969) and good accounts of the method are available in the literature only a brief description is given here.

Both ecological criteria and a new, objective test are used to study similarities between results of the three classificatory strategies applied to the same data matrix. AXOR is considered by Lambert et al. (1973) to produce divisions superior to other classificatory techniques, including association analysis, while Grunow & Lance (1969) found DIVINF preferable to association analysis on various grounds. These findings are investigated again with Bankenveld data.

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PROCEDURE

Polythetic-divisive model (AXOR)

1) Raw data

Raw data for AXOR may consist of either qualitative (presence/absence) or quantitative (cover, density, frequency, biomass) scores for each species in each quadrat. Although cover-abundance estimates were available in the present study, presence/absence data, as also used for association analysis, were used. Reasons for this decision were, firstly, that results would be more directly comparable with association analysis results, and secondly, that the presence/absence data were already coded and punched. The raw data matrix consisted of the presence of all species in the 110 Bankenveld Land System 16 m^2 quadrats.

2) Outline of AXOR

The first step in the analysis is extraction of the maximum variance axis from the data, by means of either a principal components analysis (PCA: Seal 1964) or a principal co-ordinates analysis (PCO: Gower 1966). The next step is the investigation of all (n - 1) ordered splits on the axis to find the division which gives the largest ΔI or ΔSS (see below). Improvements in the split are then made by automatic re-allocation of individuals, taken one at a time, either in absolute order on the second and subsequent axes, or by an alternative re-allocation method until the addition of a new axis order gives no further improvement. An example is outlined below.

Consider the following p species by n quadrats data matrix, where scores are either qualitative or quantitative:-

species

1, 2, 3, ... , p-1, p

1 .
2 .
3 .
$\underset{\sim}{X}$ = quadrats . .
. .
. .
n-1 .
n . . . .

For analysis by PCA, the means for each species are subtracted from the corresponding elements of $\underset{\sim}{X}$ to form matrix[19] $\underset{\sim}{Y}$. The variance-covariance matrix is then $\underset{\sim}{Y}^T\underset{\sim}{Y}$. Eigen vectors and eigen values are extracted from the variance-covariance matrix in descending order of eigen values. If $\underset{\sim}{z}_1$ is the first eigen vector then $\underset{\sim}{Y}\underset{\sim}{z}_1$ gives the component scores for the n quadrats.

(19) General accounts of matrix algebra can be found in Lawley & Maxwell (1963) and Searle (1966).

Quadrats are ranked in order of their component scores and the information drop (ΔI), or 'sum of squares' drop (ΔSS), of each possible split is calculated. Consider, for example, the following five quadrats ranked by their component scores:-

e b c a d

The following splits will be considered:-

e				b	c	a	d
e	b				c	a	d
e	b	c				a	d
e	b	c	a				d

Let the third be the split with maximum ΔI or ΔSS, whichever is being used. Each quadrat is then moved to the other side of this split in turn and an improvement in terms of ΔI or ΔSS is sought. The following moves will be made:-

a	b	c	e			d	(a moved)
e	c			a	b	d	(b moved)
e	b			a	c	d	(c moved)
b	c	d	e			a	(d moved)
b	c			a	d	e	(e moved)

Should an improvement be found, the process is started again and is repeated until stability is attained. Various strategies have been proposed to direct the moving process (e.g. based on absolute order of quadrats on second and subsequent component axes) but all yield much the same answer (S.E. Meacock[18]: pers. comm.). The moving process is a form of the automatic re-allocation process described by Grunow & Lance (1969).

For analysis by PCO, $\underset{\sim}{Y}$ is formed as above. Matrix $\underset{\sim}{W}$, corresponding to the variance-covariance matrix, is then formed:-

$$\underset{\sim}{W} = \underset{\sim}{Y}\underset{\sim}{Y}^T$$

Eigen values and eigen vectors ($\underset{\sim}{v}_i$), which are row component scores, are extracted. The 'real' eigen vectors ($\underset{\sim}{u}_i$) are then:-

$$\underset{\sim}{u}_i = \underset{\sim}{Y}^T\underset{\sim}{v}_i$$

The process then continues as described for PCA.

The correspondence between PCA and PCO is useful as it means that either the n x n (quadrats by quadrats) or p x p (species by species) matrix, whichever is smaller, may be used for the analysis. Thus, the number of species and the number of quadrats must be large before the computer's memory becomes a limiting factor.

For the analysis of Bankenveld data, PCO formulae were used as the raw data matrix contained many more species than quadrats. ΔI was used as division parameter.

3) Sums of squares

As the term 'sums of squares' is often used without sufficient definition, for example in Lambert et al. 1973, the term is briefly described here.

Sums of squares (SS), in the form of ΔSS, may be used as an alternative to the information drop (ΔI) as a measure of the goodness of a division. It has advantages over the information drop with quantitative, unbounded data[20] and may be a better general-purpose test (J.M. Lambert[21]: pers. comm.) although its properties are still being studied at Southampton.

Consider a raw data matrix with j species (j columns) and i quadrats (i rows). $\bar{x}_j$ is defined as being the mean of the jth species. The sums of squares of a given group of quadrats (A) is then given by:-

$$SS_A = \sum^{i} \sum^{j} (x_{ij} - \bar{x}_j)^2$$

(20) Bounded ecological data have defined upper and lower limits (e.g. percentage frequency:- 0-100 percent) while unbounded data need have no upper limit. Phytomass is an example of unbounded data.

(21) Address: Dr J.M. Lambert, Department of Botany, The University, Southampton, U.K.

If group A is divided into two sub-groups a and b, then:-

$$SS_A = SS_a + SS_b + \Delta SS$$

and therefore:-

$$\Delta SS = SS_A - (SS_a + SS_b)$$

Alternatively ΔSS is given by:-

$$\Delta SS = \frac{mn}{m + n} \sum^{j} (\bar{x}_j - \bar{y}_j)^2$$

where m and n are the number of individuals in sub-groups a and b and $\bar{x}_j$ and $\bar{y}_j$ are the means of the jth species in groups a and b, respectively.

4) Information statistic

The information drop, ΔI, (measured by Shannon's information statistic) on dividing group (A) into sub-groups a and b is defined as:-

$$\Delta I = \text{Icont}(A) - (\text{Icont}(a) + \text{Icont}(b))$$

where Icont(w) is the information content of group w.

Icont(w) is given by:-

$$\text{Icont}(w) = pn\underline{\ln}n - \sum_{j=1}^{p} (a_j\underline{\ln}a_j + (n - a_j)\underline{\ln}(n - a_j))$$

where <u>ln</u> is the natural logarithm and n is the number of quadrats in the group, specified by the presence or absence of p attributes. There are a_j quadrats possessing the jth attribute and $(n - a_j)$ lacking the attribute.

5) Directed search strategies

In AXOR, a PCA or PCO produces a linear arrangement of quadrats from which the optimal division is sought. A strategy such as this in which only a limited subset of all possible divisions are investigated, is known as a directed search (Williams & Dale 1965). As there are $(2^{n-1} - 1)$ possible ways of dividing n entities into two groups (Edwards & Cavalli-Sforza 1965) a directed search becomes essential with more than about 20 entities, even with the relatively powerful computers available today (Morris 1973). The directed search in association analysis is to the p possible divisions based on the p species present in one or more of the quadrats. The same directed search strategy is used by divisive information analysis (see later). In AXOR, the search is directed by reference to geometrical distances of samples along the first component of a principal components analysis or principal co-ordinates analysis.

6) Superiority of AXOR

Lambert *et al*. (1973) use a novel method for comparison of hierarchies produced from different classification models. The 'mathematically optimal' division is used as a standard with which the model being tested is compared over a large number of tests. As the mathematically optimal division is found by evaluating all $(2^{n-1} - 1)$ possible divisions, such comparisons can only be carried out on data sets of very limited size. The number of times the model under test gives the optimal division as a percentage of the number of tests is a measure of the absolute efficiency of the model under test. By using this test with classifications based on quantitative and qualitative data, Lambert *et al*. (1973) found that AXOR, with 97,6 percent success was far superior to divisive information analysis with only 59,5 percent success, when ΔSS was used to define the mathematically optimal split. Unfortunately, this technique of hierarchy comparison cannot be used with plant ecological data sets of normal size as the computations are impracticably lengthy.

Monothetic-divisive model (DIVINF)

Divisive information analysis (Lance & Williams 1968), known in this account as DIVINF, was developed as an improvement on association analysis. As it uses a divisive strategy and as each division is based on the presence or absence of a single species it is a monothetic-divisive model. Only a brief account

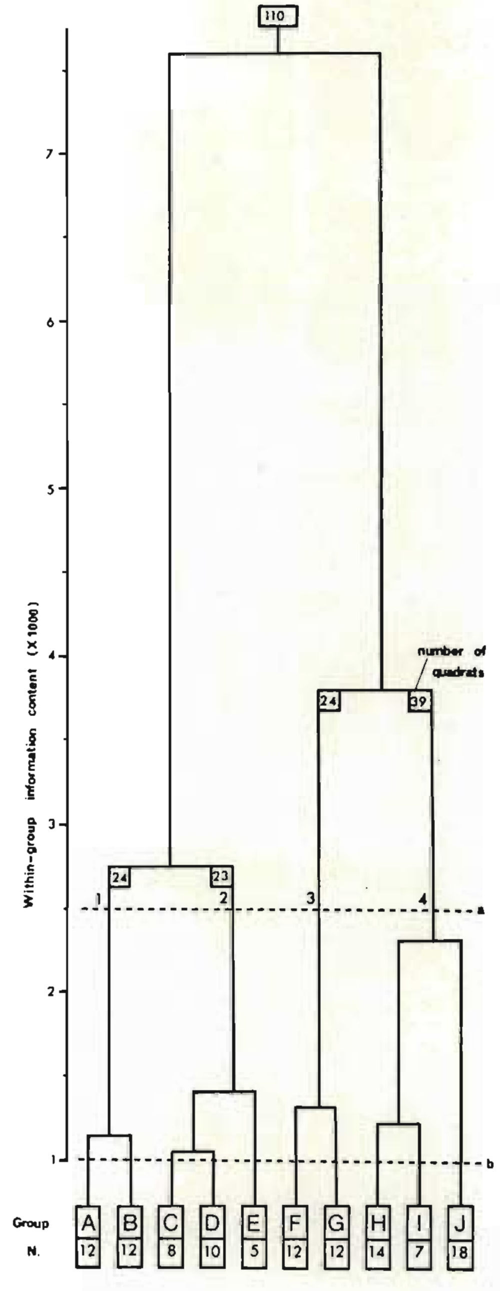

Fig. 10 AXOR classification hierarchy. N. = number of quadrats in final group. Stopping levels a and b are discussed in text.

of the procedure is given below as good accounts have been available in the literature for some time and it has been used in South Africa previously (Grunow & Lance 1969).

In DIVINF, like association analysis (AANAL), the directed search is to the p possible divisions based on the p species in the n quadrats by p species raw data matrix. The difference between DIVINF and AANAL is that the criterion for division in association analysis is the species that reduces association (X^2 in some form) by the largest amount while in information analysis the criterion is the species that produces the largest information drop (ΔI). Formulae for ΔI and Icont(w), needed for this analysis, were described in the AXOR procedure.

Data used for this DIVINF analysis were the 110 Bankenveld quadrats of 16 m^2 with species in fewer than six quadrats masked.

RESULTS AND DISCUSSION

AXOR classification

1) Statistical comparison with AANAL

The hierarchy resulting from classification of the 110 Bankenveld Land System quadrats (16 m^2) with no species excluded from the analysis by AXOR (using ΔI as division parameter) is given in Fig. 10. At within-group information content of 2500 (stopping

INSERT FIG. 10

TABLE 31 Comparison of AXOR and AANAL group constitutions at a) four-group level and b) two-group level.

a)

		AXOR classification groups				
		1	2	3	4	
AANAL groups	1	1	5	0	6	12
	2	22	10	0	1	33
	3	1	8	0	19	28
	4	0	0	24	13	37
		24	23	24	39	110

b)

		AXOR groups		
		1	2	
AANAL groups	1	38	7	45
	2	9	56	65
		47	63	110

level a), the quadrats are divided into four groups, numbered from one to four and at Icont(w) = 1000 (stopping level b) there are ten groups, labeled for convenience A through J.

At the four-group level, group constitutions of the AXOR classification and the association analysis (AANAL) classification described in Chapter 3 were compared. Results are presented in Table 31. It will be observed that AANAL Group 1 is split

INSERT TABLE 31

between AXOR Groups 2 and 4. Two thirds of AANAL Group 2 quadrats occur in AXOR Group 1 and the remainder occur in Group 2. Two thirds of AANAL Group 3 quadrats occur in AXOR Group 4. Two thirds of AANAL Group 4 occur in AXOR Group 3 and the rest are found in AXOR Group 4. In addition to following the distribution of quadrats of association analysis groups in the AXOR classification as was done above, the opposite may be done. AXOR Group 1 is virtually confined to AANAL Group 2. Nearly half of AXOR Group 2 quadrats also occur in AANAL Group 2. Other AXOR Group 2 quadrats occur in AANAL Groups 1 and 3. AXOR Group 3 is entirely confined to AANAL Group 4. Half of AXOR Group 4 quadrats occur in AANAL Group 3 and most of the rest occur in AANAL Group 4.

From the above account and from inspection of Table 31, it is obvious that the two classifications produced fairly similar quadrat groups. While the published hierarchy comparison tests to be described in Chapter 5 were not used, a new measure of

TABLE 32 Chi-square test of association between AANAL, DIVINF and AXOR classifications at four-group and two-group levels.

four-group level[a]		two-group level[b]	
classifications	X^2	classifications	X^2
AANAL - AXOR	122,3	AANAL - AXOR	54,2
AANAL - DIVINF	109,1	AANAL - DIVINF	88,1
DIVINF - AXOR	111,4	DIVINF - AXOR	73,7

[a] $p = 0{,}001$ at $X^2 = 27{,}9$ ($9^\circ f$)

[b] $p = 0{,}001$ at $X^2 = 10{,}8$ ($1^\circ f$)

association between classifications was used to obtain a quantitative measure of similarity between classifications. The new measure resulted from use of the chi-square test of association described by Bailey (1959). With nine degrees of freedom, the value of X^2 = 122,3 for comparison of AANAL and AXOR groups at the four-group level is very significant at p = 0,001 (Table 32), indicating

INSERT TABLE 32

that the two classifications are closely related.

Association at the two-group level (Tables 31 and 32) is also statistically significant at p = 0,001. At the two-group level, most AXOR Group 1 quadrats occur in AANAL Group 1 and most AXOR Group 2 quadrats occur in AANAL Group 2.

As some of the 'expected' values of the X^2 calculation are less than about five when more than four groups from each hierarchy are compared, the new test could not be used at lower hierarchical levels (Bailey 1959).

2) Final-group comparison with AANAL

A manual comparison of group constitution and hierarchy configuration was undertaken at the ten-group level of AXOR and final-group level of AANAL.

At the ten-group level, AXOR Groups A and B, are merely subsets of Diheteropogon-Schizachyrium Bankenveld, the typical community of the Bankenveld Land System. They are not discussed further. AXOR Group 3, consisting of Final Groups F and G, is totally within the fourth and final AANAL major Group. AXOR Group G includes eight quadrats of Fingerhuthia-Oropetium Bankenveld of Dolomite Sheets and four Group 7 quadrats. Although four Fingerhuthia-Oropetium quadrats are omitted, Group G is a better collection of quadrats typifying vegetation of extensive dolomite sheets than the group of the association analysis classification. AXOR Group F is a mixture of Group 7 and Fingerhuthia-Oropetium Bankenveld quadrats. Most Group F quadrats are situated on dolomite sheets but are located in a band across the northern edge of the area while most quadrats of Group G are located immediately north of Lichtenburg.

Thirteen quadrats, including all nine quadrats of Corchorus-Ursinia Bankenveld of Disturbed Sites and four quadrats of Group 7 of the association analysis hierarchy, are found in AXOR Group 4. As the AANAL quadrats are equally distributed in AXOR Groups H and I, Corchorus-Ursinia Bankenveld of the AANAL classification is not recognised by AXOR. The majority (19) of Chascanum Sandy Bankenveld quadrats occur in Groups H and J of AXOR Group 4. As six Diheteropogon-Stipagrostis Primary Bankenveld quadrats also occur in AXOR Group J, it is concluded that some Primary Bankenveld occurs on deeper, more sandy soils than are normal for the area. This conclusion could not be made from results of the association analysis. AXOR Group 2 is the most segmented group in relation to AANAL groups. Ten quadrats make up the remainder of Diheteropogon-Stipagrostis Primary Bankenveld. Of the remaining eight quadrats, most belong to Chascanum-Eragrostis racemosa Sandy Bankenveld.

TABLE 33 Floristic richness of AXOR and DIVINF groups at a) four-group and b) final-group levels expressed as mean number of species per quadrat (mean) and standard deviation of mean (SD).

Group		AXOR		DIVINF	
		mean	SD	mean	SD
a)	1	38,3	5,1	40,2	5,7
	2	42,0	6,6	40,8	5,9
	3	29,3	6,8	31,3	6,4
	4	36,4	6,3	34,8	7,6
b)	A	36,5	5,6	38,7	4,3
	B	40,1	4,0	41,7	6,5
	C	40,8	7,8	40,8	5,9
	D	42,2	6,7	29,1	8,6
	E	43,6	4,7	32,4	5,0
	F	29,5	6,1	42,0	6,3
	G	29,1	7,7	32,6	5,6
	H	33,5	6,1	29,7	6,0
	I	36,2	7,7		
	J	38,7	5,1		

3) Floristic richness of AXOR groups

Floristic richness of AXOR groups was investigated. A marked decrease in richness from left to right across the hierarchy had been found in the AANAL classifications and the pattern in AXOR groups was considered to be of interest. Results are given in Table 33. At the four-group and ten-group levels, floristically-

INSERT TABLE 33

rich and floristically-poor groups are clearly distinguished but there is no evidence of this variable's having such an over-riding influence on the analysis as there was with association analysis. Group 2 (including its Final Groups, D and E) is richest in species and Group 3 (including Final Groups F and G) is floristically poorest. Standard deviations of the mean are fairly constant and rather low throughout, suggesting that quadrats in each group have roughly the same number of species and that within-group variation in number of species per quadrat is similar in all groups.

DIVINF classification

1) Statistical comparison with AANAL

Divisive information analysis (DIVINF) results are given

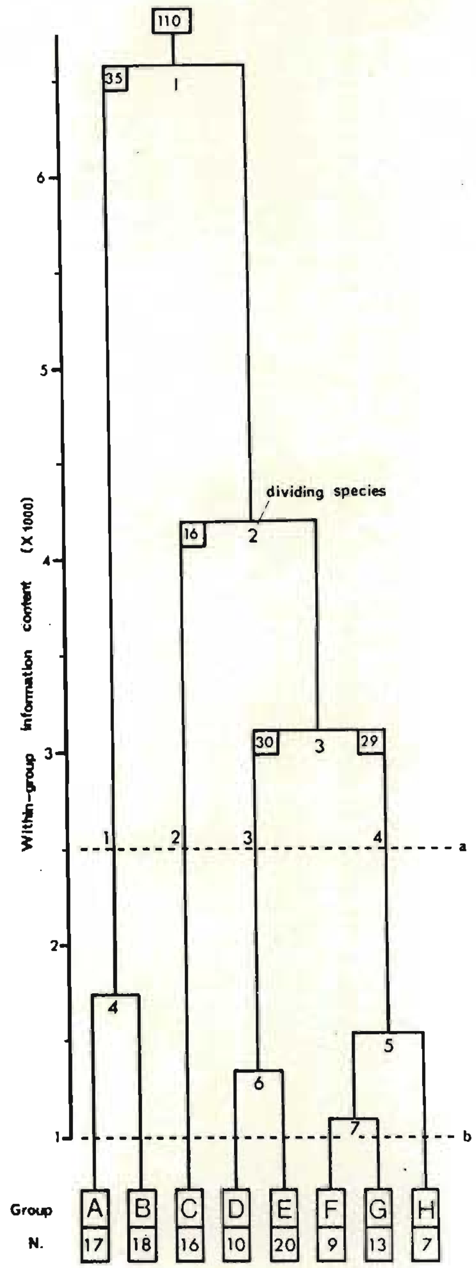

Fig. 11 DIVINF classification hierarchy. N. = number of quadrats in final group. Stopping levels a and b are discussed in text. Dividing species are: 1 = Sporobolus pectinatus, 2 = Diheteropogon amplectens, 3 = Cymbopogon plurinodis, 4 = Loudetia simplex, 5 = Justicia anagaloides, 6 = Eragrostis lehmanniana, 7 = Heteropogon contortus.

TABLE 34 Comparison of DIVINF and AANAL group constitutions at a) four-group level and b) two-group level.

a)

		DIVINF classification groups				
		1	2	3	4	
	1	6	6	0	0	12
AANAL	2	23	10	0	0	33
groups	3	6	0	6	16	28
	4	0	0	24	13	37
		35	16	30	29	110

b)

		DIVINF groups		
		1	2	
AANAL	1	45	0	45
groups	2	6	59	65
		51	59	110

diagrammatically in Fig. 11. The first division, on Sporobolus

INSERT FIG. 11

pectinatus, split off 35 quadrats on the positive side. The negative leg is split, first on Diheteropogon amplectens and then on Cymbopogon plurinodis to form four groups at I = 2500 (stopping level a). Groups are numbered one through four at this level. At a within-group information content of 1000 (stopping level b) eight groups exist, labeled A through H, to facilitate group identification in the following discussion.

Although the similarity between the association analysis (AANAL) classification of Chapter 3 and the DIVINF classification was apparent from inspection of the two hierarchies, it was clear that similarities in group constitution were not as great as those between AANAL and AXOR. A two-way table was drawn up to compare more accurately DIVINF and AANAL groups at four- and two-group levels. In Table 34 the number of quadrats common to each

INSERT TABLE 34

pair of DIVINF and AANAL groups is given. From Table 34 it is apparent that AANAL Group 1 is equally divided between DIVINF Groups 1 and 2. Two thirds of AANAL Group 2 quadrats occur in DIVINF Group 1 and the rest in Group 2. Over half of AANAL Group 3 occurs in DIVINF Group 4 and the rest of the quadrats are divided between DIVINF Groups 1 and 3. Two thirds of AANAL Group 4 occurs in DIVINF Group 3 and one third in DIVINF Group 4.

Thus, inspection of the two-way table between hierarchies at the four-group level also indicated similarities between the classifications. The new chi-square test of association was carried out on this two-way table as well. The result (Table 32) is significant at p = 0,001, indicating that the groups delimited by AANAL are very significantly related to groups delimited by DIVINF. As the X^2 value for AANAL-DIVINF is lower than for AANAL-AXOR (Table 32) it is concluded that the former pair of classifications are not as similar as the latter. As some of the 'expected' values in the X^2 equation were rather low, the calculation was repeated at the two-group level (Tables 34 and 32). A significant X^2 (p = 0,001) was obtained again.

2) Final-group comparison with AANAL

AANAL Group 1 (Diheteropogon-Stipagrostis Primary Bankenveld) occurs in DIVINF Groups B and C. Groups 2a, 2b and 2c of AANAL Group 2 (Diheteropogon-Schizachyrium Bankenveld) occupy the remainder of DIVINF Group 1. Group 2d (also Diheteropogon-Schizachyrium Bankenveld) forms a clear sub-group within DIVINF Group C.

A small part of AANAL Group 3 (Chascanum-Eragrostis racemosa Sandy Bankenveld) is found in DIVINF Group B and the remainder occurs with AANAL Group 4 (Chascanum-Anthephora pubescens Sandy Bankenveld) in DIVINF Group 4, in Final Groups F and G. AANAL Group 5 (Corchorus-Ursinia Bankenveld of Disturbed Sites) is a small group of only 9 quadrats, which occur scattered through DIVINF Group 4. Fingerhuthia-Oropetium Bankenveld of Dolomite Sheets (AANAL Group 6) occurs partly in Group 3 (Final Group D) and partly in Group 4 (Final Group H) of the DIVINF hierarchy. AANAL Group 7 occurs mainly in DIVINF Groups D and E.

3) Floristic richness of DIVINF groups

DIVINF, like AXOR, is not sensitive to quadrat floristic richness. Means and standard deviations of the number of species per quadrat for each group are given in Table 33. Groups 1 and 2 are slightly richer in species than Groups 3 and 4 at the four-group level. At the eight-group level, certain groups, including B, C and F, are floristically-rich while others, like D and H are floristically-poor. A gradient from floristically-rich to floristically-poor groups across the hierarchy is not present. In general, the lower the mean number of species per quadrat the higher the standard deviation and vice versa, indicating that floristically-rich groups have a more constant number of species per quadrat than floristically-poor groups.

Comparison of AANAL, AXOR and DIVINF results

Brief comparisons of AANAL results from Chapter 3 with AXOR and DIVINF classifications have been made. To make a comparison between all three models possible, DIVINF and AXOR group constitutions are compared at four- and two-group levels in

TABLE 35 Comparison of DIVINF and AXOR group constitutions at a) four-group level and b) two-group level.

a)

		AXOR classification groups				
		1	2	3	4	
	1	21	14	0	0	35
DIVINF	2	3	6	0	7	16
groups	3	0	0	19	11	30
	4	0	3	5	21	29
		24	23	24	39	110

b)

		AXOR groups		
		1	2	
DIVINF	1	44	7	51
groups	2	3	56	59
		47	63	110

Table 35. Results of the new chi-square test of association

INSERT TABLE 35

between these classifications are given in Table 32, together with the other chi-square test results.

At the four-group level, AANAL is more similar to AXOR than is DIVINF. At the two-group level, the two monothetic-divisive strategies are most similar while they are least similar at the four-group level. AXOR is more similar to DIVINF than to AANAL at the two-group level. As all the associations are statistically very significant not much weight can be attached to differences of degree outlined above.

CONCLUSION

While brief comparisons of AXOR and DIVINF classifications with AANAL final groups were made, detailed interpretations of AXOR and DIVINF results were not given. AANAL, which was interpreted in detail, had given a sufficiently meaningful classification of the quadrats, with the result that two more detailed interpretations were considered to be unnecessary. Differences between DIVINF and AANAL and AXOR and AANAL were shown to be statistically not significant by a X^2 test of association, not previously used to compare classifications.

A degree of similarity between the results was expected, merely because the same raw data matrix was used for all three analyses, but the reason for AXOR's being slightly more similar to AANAL than DIVINF is not clear on the basis of strategies used or rare species masks employed. AANAL and DIVINF are both monothetic-divisive models while AXOR is a polythetic-divisive model. The same mask of rare species was used for AANAL and DIVINF and no species were excluded from the AXOR analysis. DIVINF, and the AXOR model used for the present study, both used the information statistic as division parameter.

Some AXOR groups represented improvements on AANAL groups while some were less easy to interpret in the context of AANAL groups. Some conclusions resulting from classification by AXOR after AANAL could not have been reached from AANAL alone. Both AXOR and AANAL yield satisfactory classifications of the quadrats, provided that groups are interpreted intelligently.

It is concluded, finally, that the three classifications are basically very similar, even though association analysis is sensitive to floristic richness of quadrats and the other models are not. This conclusion means that either the vegetation is very easy to classify automatically, or that all three models are robust. As all three models give similar results and these results were ecologically meaningful, it may be safely assumed that all are good ecological classifications of the vegetation. It should be borne in mind, however, that AXOR and DIVINF do not seem to be sensitive to floristic richness and that AXOR is preferred by Lambert et al. (1973) on the basis of experimental comparisons.

CHAPTER 5

D A T A R E D U C T I O N A N D O B J E C T I V E C O M P A R I S O N O F A U T O M A T I C C L A S S I F I C A T I O N S

INTRODUCTION

Divisive information analysis (DIVINF) was applied by Grunow & Lance (1969) to data from Soutpan in the Transvaal Bushveld. Using ecological and physiological validity of subdivisions as tests, DIVINF was preferred by these authors to association analysis of the same data (Grunow 1965a) in both the normal and the inverse forms. That paper is probably the only published South African comparison of two automatic classification techniques.

In nearly all other comparisons of techniques (including Dale 1960, Williams, Lambert & Lance 1966, Lambert & Williams 1966, Austin & Greig-Smith 1968, Moore et al. 1970, Pritchard & Anderson 1971 and Boucher 1972) subjective ecological assessments are used to compare results, although at least four methods have been developed for the quantitative comparison of groups formed in classifications as well as for comparison of the hierarchies themselves. The advantages of numerical methods of comparison are that they are objective, they give a statistical estimate of significance and they can be calculated in a fraction of the time required to make ecological interpretations of two classifications.

Before the rapid increase in the number of classificatory procedures, which was briefly mentioned in Chapter 4, and the following need to compare results, Goodman & Kruskal (1954, 1959) outlined some general approaches to the problems of cross-classificatory comparison. They were particularly concerned with associations between classifications in a broad sense and influenced later work in this field.

Sokal & Rohlf (1962) were the first biologists to point out the need for an objective comparison technique. They considered that with the increasing acceptance of numerical techniques an experimental phase involving the use of various types of coefficients was beginning. The experiments would involve the comparison and evaluation of results from many classifications of the same data. Their cophenetic correlation technique was developed to this end for numerical taxonomists. It is based on the correlation between the hierarchical levels at which each pair of quadrats is united in each classification. Williams & Clifford (1971) pointed out its shortcomings (see below) and described an improved technique which distinguishes differences in group composition from differences in configuration of the hierarchy. Configuration is the route connecting two quadrats within the hierarchy. Comparison techniques which consider only group composition have been described by Williams et al. (1969) and Orloci (1970). As these objective tests had been developed, the writer considered at the outset that these, as well as subjective, ecological interpretation should be used to compare results of classifications.

The influence of data reduction on the hierarchy resulting from use of the same classification strategy was studied at the same time as objective comparisons were investigated. Data reduction is the omission of species or the exclusion of quadrats from data before classification. In agreement with Dale (1960), the writer considers that it is always preferable to use the largest possible number of quadrats so that in this study, as in that of Dale, only reduction of species is considered.

Data reduction is usually undertaken for pragmatic reasons. When computer time is expensive, data reduction may result in a large saving of money, time in the field may be saved by certain forms of data reduction or, thirdly, reduction may be necessary so that the data matrix will fit into the computer memory. Although it is widely assumed that data reduction has an insignificant effect of the subsequent analysis, and data are often reduced on this assumption, little is known about the stability of classifications with various degrees of reduction and whether reduction can be justified on grounds other than the pragmatic ones given above. The writer set out to investigate this assumption.

REVIEW OF COMPARISON METHODS

Group comparison methods: COMPAR and INFOR

1) COMPAR method

Williams et al. (1969) define and use a measure of **similarity** between two classifications, referred to in this account as COMPAR. It is also used by Tracey (1969). COMPAR is based on a technique described by Rayner (1966) and provides a measure of group similarity.

COMPAR is based on the coefficient of floral community, defined in conventional (a, b, c, d) notation of a 2 by 2 contingency table as 2a/(2a + b + c). For two groups, x and y, one from each classification, the number of quadrats common to both groups is a, the number in x but not in y is b, and the number in y but not in x is c. Let there be m groups in the first classification (A) and n in the second (B). The first A-group is compared with each B-group in turn and the largest coefficient of floral community is retained, irrespective of which B-group produced it. The process is repeated for the remainder of the A-groups. The process is then reversed, each B-group being taken in turn as referent. The mean of the (m + n) largest coefficients is the measure of similarity between the two classifications.

2) INFOR method

Orloci (1970) developed a test criterion for independence between two classifications, referred to in this account as INFOR. It is the second measure of group similarity to be described. INFOR is the error component commonly used in connection with the analysis of contingency tables and is based on the information statistic.

Suppose there are m groups in the first classification and n in the second. The number of quadrats possessed in common by the ith group of the first and jth group of the second classification (x_{ij}) is found for each i and j. The symbols X, X_i and X_j represent the grand total, the ith row total and the jth column total respectively, in the margins of the x_{ij} contingency table. The information statistic (2I) is then given by:-

$$2I = 2 \sum_{i=1}^{m} \sum_{j=1}^{n} x_{ij} \ln \frac{Xx_{ij}}{X_i X_j}$$

where ln is the natural logarithm. 2I is approximately distributed as chi-square with (m - 1)(n - 1) degrees of freedom under the null hypothesis that the two classifications are independent.

Group and configuration comparison methods: COPHEN and WILLCLIFF

1) COPHEN method

The technique of cophenetic correlation, known in this account as COPHEN, was developed by Sokal & Rohlf (1962) and is also described by Sokal & Sneath (1963). Configuration as well as group constitution are taken into account by COPHEN.

Consider, for example, an association analysis hierarchy in which H.S.X^2 values[13], are plotted on the ordinate, as measures of group homogeneity. As the number of groups increases from the top of the hierarchy to the bottom, H.S.X^2 values generally decrease while group homogeneity increases proportionally. Cophenetic value would then be defined as the H.S.X^2 value at which the branches connecting a given pair of quadrats unite. The closer the relationship between two quadrats, the lower will be their cophenetic value in this example. Cophenetic correlation is then the product moment correlation coefficient, calculated over all corresponding cophenetic values from a pair of classifications. Statistical significance of the correlation is not applied by Sokal & Rohlf; only the magnitude of the value is used as a measure of similarity.

Cophenetic correlation may be calculated between any two hierarchical classifications (agglomerative and divisive) for which measures of group homogeneity or group similarity have been used on the ordinate of the hierarchies. Depending on whether the measures increase or decrease from top to bottom of the hierarchies, cophenetic correlation may be either positive or negative.

2) Shortcomings of COPHEN method

Williams & Clifford (1971) show that COPHEN has two shortcomings, which make it unsuitable for the truncated, intensely-clustering classificatory strategies now in common use. They consider, firstly, that it is unable to distinguish between changes due to group composition and changes due to configuration of groups within the hierarchy (even though it is a measure of both these properties). Secondly, it is sensitive to the convention used for representing the hierarchy in two dimensions. They present a revised strategy, referred to in this account as WILLCLIFF, which they consider, overcomes these two drawbacks. An almost identical method was proposed independently by Phipps (1971).

Williams & Clifford (1971) point out that it is now common practice not to consider a hierarchy down to the level of individual elements but that the hierarchy is usually truncated at a convenient number of groups. All members of each group are then regarded as being the same. Classifications may then differ in two ways. Firstly, group membership might remain unchanged but the position of a group in the hierarchy might change (configurational change). Secondly, closely-related groups may interchange some of their members with minimum disturbance to the hierarchy (constitutional change). Knowledge of changes in both the constitution and the configuration of groups is required. While Goodman & Kruskal (1954, 1959) describe methods for comparing constitution alone, Williams & Clifford (1971) consider that the measure must be at least approximately additive over both constitutional and configurational changes.

Williams & Clifford (1971) consider the second shortcoming of COPHEN, outlined below, to be more fundamental. The level of fusion or division in a hierarchy was originally defined by the homogeneity value (H.S.X^2, $\triangle$I, Icont(w)) at which that fusion or division occurred. According to Williams & Clifford (1971), although homogeneity measures are used in the construction of hierarchies, they are not an integral part of their definition and should therefore not be used in the measure of hierarchy comparison.

3) WILLCLIFF method

WILLCLIFF is acknowledged by its describers (Williams & Clifford 1971) to be no more than a variant of COPHEN. It has two features which, they consider, represent advantages over COPHEN. Firstly, it uses only the invariant properties of the hierarchy, making it independent of the method of presentation. Secondly, it is substantially additive over group composition and configuration, as is required of such a measure. It is used for the comparison of three numerical taxonomy classifications by Clifford & Williams (1973).

For a given pair of quadrats in two classifications, the number of nodes that separate them in each hierarchy is denoted by m_1 and m_2, respectively. The difference (d) between the two, say $m_1 - m_2$, is found. The order of subtraction is immaterial as long as the subtraction is done consistently. The process is repeated for all n(n-1)/2 pairs of quadrats. The difference, d, may be positive (d+), negative (d-), or zero. Positive and negative differences are accumulated separately. The sum (D) of the absolute values of d+ and d- is a measure of the total changes in the hierarchy as one moves from one classification to the other. D is best scaled by reference to the n(n-1)/2 pairs which have contributed to it so that the final measure (f) takes the form:-

$$f = 2D/n(n-1)$$

If the classifications under study are truncated, a pair whose members are in the same group in a given classification will have zero m for that classification. In the course of obtaining D, it is easy to count the number of cases for which m is zero in one classification but not the other. These two counts are accumulated separately and denoted as g+ and g- and the sum of their absolute values by G. G is then a measure of the total number of transfers between groups.

Unless D and G are both zero, the hierarchies being compared are not identical. Although D and G are related, the relationship is not simple. Clifford & Williams (1973) regard the two measures as independent. Although D may change without influencing G, any change in G results in a change in D.

PROCEDURE

Two divisive-monothetic classification models, divisive information analysis (DIVINF) and association analysis (AANAL), and three methods of data reduction were used in this study. Firstly, the influence on the resulting classifications of masking three levels of rare species from quadrats of the same size, as opposed to not masking any species in a control analysis, was studied using DIVINF. Secondly, the influence on the resulting classifications of four different quadrat sizes and two levels of reduction in the number of species in each quadrat were investigated using AANAL.

For all classifications, raw data were presence of species in the 110 Bankenveld Land System quadrats. In all DIVINF classifications, quadrat size was constant (16 m^2) while in all AANAL classifications a standard mask of all species occurring in fewer than six quadrats was used.

Elimination of rare species: four DIVINF classifications

DIVINF was used for classification of 16 m^2 quadrats with no species masked, with species present in one and two quadrats masked, with species present in five or fewer quadrats masked and with species present in 10 or fewer quadrats masked. In the following presentation of results and discussion, these classifications are referred to as g, h, i and j, respectively.

<u>Reduction in quadrat size and floristic richness: six AANAL classifications</u>

In AANAL classifications, differences under test were, partly, the size of quadrat and, partly, the number of species used from each quadrat. Four different quadrat sizes and two degrees of reduction in the number of species in each quadrat were used in a total of six analyses.

As described in Chapter 3, triangular samples with areas of 4 and 8 m^2, and square samples of 16 and approximately 64 m^2 were available. For economy of reference, the four association analyses based on samples of these sizes are referred to as: 4SQM, 8SQM, 16SQM and 64SQM, respectively.

It was found that 19 was the smallest number of species recorded in a 64 m^2 sample. This figure was taken and an association analysis was carried out using the first 19 species recorded from each sample. This data reduction was possible as species had been recorded in order of encounter (Chapter 3). As a further, and extreme data reduction, an analysis was carried out using only the first 12 species recorded from each sample. During field work it was noticed that there were usually 10 to 12 conspicuous species, which could be recorded before a detailed search of the quadrat was begun. These analyses are referred to below as F19 and F12, respectively.

The term, floristic richness, is used for the number of species recorded in a quadrat. Reduction in floristic richness is then reduction of the number of species in each quadrat. In

TABLE 36 Information statistics (2I) of INFOR comparisons of four DIVINF classifications at four-group and final-group levels. All values are significant at p = 0,001 (see text).

	four-group level				final-group level		
	h	i	j		h	i	j
g	157	157	157	g	478	442	379
h		225	225	h		477	414
i			297	i			499

g:- no species masked

h:- 1 to 2 frequency-species masked

i:- 1 to 5 frequency-species masked

j:- 1 to 10 frequency-species masked

this study the number of species was reduced to a constant but it could also have been reduced by a constant percentage of the total number of species in each quadrat.

RESULTS

Elimination of rare species

Two hundred and eleven species were included in DIVINF classification g, which took 1960 seconds of computer time (ICL 1907, 64K computer). Thirty one percent of the species (i.e. 66 species) were masked in h, which took 1540 seconds to compute. Forty four percent (92 species) and 55 percent (115 species) of the species were excluded in i and j, respectively, which took 1240 and 1020 seconds of computer time.

1) INFOR comparison

INFOR was applied to groups formed from the four DIVINF hierarchies at the four-group and final-group (nine, or fewer, quadrats not divided further) levels (Table 36). In Table 36

INSERT TABLE 36

478 is, for example, the value of 2I for classification g (no species masked) in comparison with h (species present in one

and two quadrats masked) at the final-group level. The value 157 is 2I for the comparison of the same pair of classifications at the four-group level. As 2I is approximately distributed as X^2 (11), the significance of these results may be evaluated by reference to the X^2 table of Fisher & Yates (1963). At the four-group level there are nine degrees of freedom and significance may be evaluated in this way but at the final-group level there are more than 250 degrees of freedom and the formula:-

$$(2X^2)^{\frac{1}{2}} - (2n - 1)^{\frac{1}{2}}$$

with n equal to the number of degrees of freedom, is used as a normal deviate with unit variance for evaluating significance (Fisher & Yates 1963).

All results (Table 36) are significant at $p = 0,001$, indicating very significant associations between all pairs of classifications (Orloci 1970). In the following discussion, the magnitude of 2I is used as a measure of association, or similarity, even though all values are statistically equal. At both stopping levels, classifications i and j are the most similar while h and i are also similar at both levels. Although still very significantly associated, the most dissimilar pairs at both levels are g and i, and g and j.

These results indicate that increasing the mask of rare species from none masked to species in 10 or fewer quadrats masked does not cause a statistical difference to group composition at either a high or a low hierarchical level. Differences between

TABLE 37 Results of COMPAR comparisons of six AANAL hierarchies at four hierarchical levels. Highest values at each level are underlined and lowest values are marked '.

	two-group level					three-group level				
	16SQM	8SQM	4SQM	F19	F12	16SQM	8SQM	4SQM	F19	F12
64SQM	79	80	86	88	84	66	66	64	62	71
16SQM		96	81	76	72'		69	60	57'	59'
8SQM			80	77	74'			63	55'	63
4SQM				79	75'				57'	61
F19					96					69

	four-group level					H.S.X^2 = 10,0 level				
	16SQM	8SQM	4SQM	F19	F12	16SQM	8SQM	4SQM	F19	F12
64SQM	57	55	54	54	57	56	48	37'	46	39'
16SQM		60	48'	52'	51'		54	45	45	43'
8SQM			50	54	51'			44'	46	43'
4SQM				46'	49'				43	36
F19					57					59

hierarchies increase as more species are masked but once a certain number have been masked, a larger mask has little effect on group composition.

Reduction in quadrat size and floristic richness

Out of a total of 223 species occurring in quadrats of 64 m^2, 97 were masked as they occurred in fewer than six quadrats. Similarly, with the 16, 8 and 4 m^2 samples, 92, 89 and 79 of the 211, 191 and 172 species were masked before classification. Relatively few species were included in classifications F19 and F12. Of the 172 species recorded at least once in the first 19 species of each quadrat, 88 occurred in fewer than six quadrats and of the 140 species recorded in the first 12 species of each quadrat, 74 occurred in fewer than six quadrats and were therefore masked before analysis, leaving 84 and 66 species for the F19 and F12 analyses, respectively.

1) COMPAR comparison

Results of COMPAR comparisons of the six AANAL classifications are presented in Table 37. Comparisons were made at the two-group,

INSERT TABLE 37

three-group, four-group and H.S.X^2 = 10,0 levels. In Table 37, 79 is the measure of group similarity between analyses of 64SQM and 16SQM data sets at the two-group level, measured by the technique of Williams et al. (1969). Thresholds for high and low values in Tables 37, 38 and 39 were chosen arbitrarily.

The general decrease in similarity as the number of groups increases is evident. The drop in similarity from the two-group to three-group levels is largest. Hierarchy pairs that retain their high similarities at all four levels include F19 and F12, the two analyses where floristic richness is the same in all quadrats, and 16SQM and 8SQM. At three levels, 64SQM results are similar to 16SQM results and at one or more hierarchical levels 64SQM is similar to all other analyses. The 4SQM sample has only one high similarity value. At the 2-group level it is similar to the 64SQM hierarchy.

Most low similarity values are found in hierarchy pairs in which F12 is one of the pair. Low similarities are also found in pairs having the 16SQM and 4SQM data sets as one of the pair.

As COMPAR measures similarity of group constitution, results relate only to similarities between groups existing at each hierarchical level. The first result, namely that similarity decreases as the number of groups increases, is to be expected. A larger number of differences are obviously likely with a greater number of groups.

An important finding is that the classification based on 12 species per quadrat was generally most dissimilar from all the other classifications with regard to group constitution. It is possible that the classification is more unstable and has many more misclassified or differently placed

TABLE 38 Information statistics (2I) of INFOR comparisons of AANAL hierarchies at 5-group level. $p = 0{,}001$ at $X^2 = 39{,}3$ ($16^o f$) (See Table 37 for explanation of symbols).

	16SQM	8SQM	4SQM	F19	F12
64SQM	136	<u>143</u>	116'	<u>146</u>	118'
16SQM		<u>163</u>	128	136	101'
8SQM			89'	<u>149</u>	133
4SQM				116'	87'
F19					<u>176</u>

quadrats than other classifications. The similarity between the two analyses with constant floristic richness, however, suggests that a different, but stable, classification results from that where floristic richness is variable.

On the other hand, the similarities between the 64SQM data set and all the others and the similarity between the 16SQM and 8SQM data sets suggest that 16 m^2 is an adequate sample size while 4 m^2 is possibly not large enough for this vegetation. Although the aim of the present study was not the determination of optimal quadrat size, similar results were obtained by J.C. Scheepers[1] during pilot studies for the Highveld Ecological Survey.

2) INFOR comparison

Results of comparing the six AANAL hierarchies at the 5-group level by INFOR are given in Table 38. All similarities

INSERT TABLE 38

are significant at p = 0,001, indicating that groups from all hierarchies are statistically very similar. In the following discussion the magnitude of 2I is taken as a measure of similarity. The two classifications with constant floristic richness (F19 and F12) are most similar (2I = 176). The 64SQM data set is similar to the 8SQM and F19 sets. The 8SQM set is also similar to the 16SQM and F19 sets. The 4SQM set has low

TABLE 39 Results of a) COPHEN (r) and b) WILLCLIFF (f) comparisons of AANAL classifications at five-group level (See Table 37 for explanation of symbols).

a)

	16SQM	8SQM	4SQM	F19	F12
64SQM	0,36'	0,49	0,60	0,58	0,57
16SQM		0,65	0,35'	0,24'	0,26'
8SQM			0,45	0,37'	0,46
4SQM				0,40	0,43
F19					0,84

b)

	16SQM	8SQM	4SQM	F19	F12
64SQM	1,18	1,01	1,11	1,50	1,26
16SQM		0,69'	1,07	1,10	0,90'
8SQM			0,93'	1,21	0,84'
4SQM				1,28	0,97
F19					0,98

similarity with (but is still significantly similar to) all other classifications except 16SQM. F12 is different from 64SQM and 16SQM classifications.

According to the information statistic, then, group constitution is highly correlated over all 15 comparisons. Furthermore, these results are similar to those of COMPAR. Most highly correlated are F12 and F19 sets and the 4SQM set is least highly correlated with all other analyses. The F12 set also differs from the two sample sizes with largest areas (64SQM and 16SQM).

3) COPHEN and WILLCLIFF comparisons

Results of COPHEN and WILLCLIFF comparisons are given in Table 39. By cophenetic correlation (COPHEN), F19 and F12 data

INSERT TABLE 39

sets are the most similar by far. The 64SQM data set is similar to the 4SQM, F19 and F12 sets and the 16SQM set is similar to the 8SQM set. The most dissimilar data sets are 16SQM compared with F19 and F12 sets. The 64SQM and 16SQM pair and the 16SQM and 4SQM pair are also dissimilar.

A rather different result is shown by WILLCLIFF (Table 39), where the smaller the f-value the greater is the similarity between classifications. The 16SQM and 8SQM pair are similar by this measure as well but the F12 and F19 pair has dropped

TABLE 40 Correlation coefficients between measures of similarity.

	COMPAR	WILLCLIFF	COPHEN
INFOR	0,64^{++}	0,02	0,50^{+}
COMPAR		-0,11	0,57^{+}
WILLCLIFF			-0,12

$^{+}$p = 0,05 at r = 0,48 (n = 15)

$^{++}$p = 0,01 at r = 0,61 (n = 15)

from being the most similar in COPHEN to sixth (out of 15) in WILLCLIFF. The most dissimilar pair by WILLCLIFF (64SQM and F19) is the fourth most similar by COPHEN.

4) Correlations between methods of comparison

In view of the marked disagreement between results of COPHEN and WILLCLIFF measures, correlations between results of all comparison techniques were calculated. Product moment correlation coefficients were calculated between the results of each pair of similarity measures, over the 15 classifications. The four-group level of COMPAR results were compared with five-group levels of WILLCLIFF, COPHEN and INFOR results.

Correlations are given in Table 40. At the five percent level

INSERT TABLE 40

of significance, INFOR and COMPAR, INFOR and COPHEN, and COMPAR and COPHEN are positively correlated. Negative correlations are expected between WILLCLIFF and the other measures as the more similar two classifications are, the smaller is the WILLCLIFF measure (f) and the larger is the other measure. Although WILLCLIFF and COMPAR, and WILLCLIFF and COPHEN are negatively correlated, values are far from being statistically significant.

As INFOR and COMPAR are both group-comparison techniques the strong correlation between them is expected. The correlation between COPHEN and the two group-comparison methods indicates that all three techniques are measuring similar, or related, properties of the classifications. The low correlation between WILLCLIFF and the other three measures suggests that the former is a measure of a property of the hierarchies very different from the property measured by the other three measures. This finding is surprising in view of the statement by Williams & Clifford (1971) that WILLCLIFF is merely a modification of COPHEN.

DISCUSSION AND CONCLUSIONS

Four methods for the automatic comparison of hierarchies, COMPAR, INFOR, COPHEN and WILLCLIFF, have been described in detail, as they are not well-known in South Africa and it is unlikely that any have been used in South Africa. Not one of the four methods has been used extensively at all and no account of comparisons between results of the methods is known. Most techniques are described and used once, or at most twice, in the literature before being abandoned. Even though relatively few objective comparisons are made in this study and the work is incomplete, it is unlikely that as many different comparison methods have previously been used on the same set of automatic classifications.

After DIVINF had been used on three data sets with rare species eliminated, Austin (1972) pointed out that association analysis is markedly sensitive to rare species while divisive information analysis is not. Therefore, as it was the rare species which were varied in this study, the result obtained, namely, stability of group composition would be expected with DIVINF but not with AANAL. It is unfortunate that Austin's statement was not tested by carrying out a number of AANAL classifications with different percentages of rare species masked. It is also regretted that no other DIVINF classifications were available for comparison. Knowledge of its performance in data of uniform species richness (F12 and F19 data sets) would be valuable, particularly as Field (1969) has pointed out that the information statistic is symmetric with respect to zero. This means that quadrats with a large number of zeros in common would appear similar. In the F12 and F19 data sets, species richness is identical throughout and therefore other factors, if any, would influence the classification.

Automatic comparison techniques are of use for comparing two classifications. Provided an in-depth study can be made at every hierarchical level with both the same number of groups in each classification and with the same hierarchical stopping levels, useful results may be obtained. Choice of only one or two levels is not sufficient. Where more than two classifications are involved, however, the amount of computation increases very rapidly.

As results of three comparison techniques were found to be strongly correlated, it would be logical to choose one of them for future comparisons. The choice is, however, rather difficult. At first, INFOR may appear to be the most suitable. In addition to measuring similarity it provides a statistical test of the significance of the similarity, but although further testing will be required, it seems too insensitive to degrees of dissimilarity (all 15 results significant at p = 0,001: Table 38). As no test of significance is given by COMPAR, only COPHEN remains as a test of similarity. Williams & Clifford (1971), however, point out two serious shortcomings of COPHEN. Not one of the three methods is therefore acceptable. The comparison method developed and used in Chapter 4 is also not suitable as a general test as values in the contingency table become too small if the number of groups is increased above about four with 110 quadrats.

The lack of correlation between WILLCLIFF and the other measures suggests that, while it may be used for the reasons given by Williams & Clifford (1971), it should not be used alone.

It is concluded that a new technique is necessary for the automatic comparison of classifications. Ideally, the new technique should consider group composition and group configuration at all hierarchical levels simultaneously. Such a technique does not exist at present and until it is developed the quantitative comparison of classifications will have only limited usefulness.

Data reduction of some kind has been used in virtually every automatic classification carried out in South Africa although it is unlikely that its influence has been investigated to this degree of detail before. It was shown in this Chapter that data reduction of various kinds, and including fairly severe levels of reduction, has remarkably little effect on the resulting classification when objective methods are used to compare classifications. This conclusion is most important as data reduction does save computer time and therefore computing costs (see: Results of elimination of rare species, above) and as it would save time in the field to have to record only a limited number of species in each quadrat (F12 and F19 analyses). It will be unwise, however, to limit the recording of species in a sample to a fixed, small number as it is easy to record, consciously or subconsciously, well-known or conspicuous species only, which could lead to erroneous data and results.

CHAPTER 6

STUDY OF BANKENVELD BY THE ECOLOGICAL PROFILES TECHNIQUE

INTRODUCTION

Automatic classification of vegetation, as described in earlier Chapters, is only one of a number of ecological synthesis techniques that can be applied to ecological data. The synthesis technique which is usually the first to be applied to ecological data at the Centre d'Études Phytosociologiques et Écologiques Louis Emberger (C.E.P.E.) at Montpellier, France, is that of Ecological profiles and information shared between species and ecological variables (Profils écologiques et information mutuelle entre espèces et facteurs écologiques) (Morris 1973, Romane *et al.* 1973). The name is generally shortened to 'Ecological profiles'. The technique, which is univariate, is described and results of its use are given in this Chapter. Its main application by French ecologists is for improvement of sampling but it can also be used for elucidating species reactions to environmental variables. It has not been used in South Africa before.

The first account of the method was given by Godron (1965) and since then more detailed descriptions have been prepared by Godron (1968), Daget et al. (1972) and Guillerm (1969a, b, c, 1971), all of which have been in French. Recently, Morris & Guillerm (1973) prepared the first English description of the technique. As no simple, step-by-step explanation of the method is yet available in English, such an explanation is given here. The 110 Bankenveld Land System quadrats are used to illustrate the utility of Ecological profiles.

PROCEDURE

Type and treatment of data

Both floristic data (presence of species) and habitat data (multi-state, or continuous variables converted to multi-state) from samples are required.

1) Floristic data

Floristic data were the same as those for association analysis (Chapter 3) before rare species were masked. Presence data of all 211 species in 16 m^2 quadrats were used.

2) Habitat variables

The 12 habitat variables listed in Table 41 were coded for

TABLE 41 Ecological variables used in the analysis and number of classes of each.

Code No.	Variable	No. of classes	No. of classes after grouping
1.	Topographic position	8	8
2.	Aspect	7	3
3.	Slope	3	3
4.	Biotic influence	4	4
5.	Surface rock	4	4
6.	Soil depth	11	6
7.	Soil pH	4	4
8.	Soil HCl reaction	2	2
9.	Soil colour (Munsell)	10	6
10.	Total basal cover	4	4
11.	Basal cover stratum II	8	7
12.	Basal cover stratum IV	8	6

analysis. The first eight are acceptable habitat variables and as

INSERT TABLE 41

soil colour (the ninth variable) is considered an important indicator of soil internal drainage it is also acceptable as a variable. Total basal cover (variable 10) was that of all grasses and herbs combined, whereas strata II and IV (variables 11 and 12) are those defined by Godron et al. (1968), namely, stratum II is from five to 25 cm tall and stratum IV is from 50 to 100 cm tall. An English summary of the standardized habitat variable coding system used by Montpellier ecologists is given by Godron & Poissonet (1970). For the present purpose, basal cover was considered to be an environmental variable whereas it is usually considered to be a structural property of the vegetation. Cover was used in this way as so few habitat variables had been measured.

As the variables had not been recorded for analysis by Ecological profiles, not enough information was always available to be coded according to the specifications of Godron et al. (1968). Topographic position, apparent biotic influence, soil pH and soil HCl reaction were, however, coded according to their specifications. Aspect, soil depth and soil colour were coded in the same way but the total number of classes was reduced later in the analysis. As there is little topography in the Lichtenburg area a special scale, which follows, was used for slope: 0 = no slope, 1 = slight (less than 1%), 2 = 1% or more. Amount of rocky substrate exposed in the quadrat was coded as: 1 = none, 2 = little, 3 = moderate, 4 = much.

TABLE 42 Comprehensive profile for a variable with K classes.

	class 1	class 2	class 3	......	class K	Total
			Number of quadrats			
ecological variable	R_1	R_2	R_3	....	R_K	$N=\sum_{i}^{K} R_i$

Total basal cover was recorded on the following scale:
2 = 5,0 - 9,9%, 3 = 10,0 - 14,9%, 4 = 15,0 - 19,9%, 5 = 20,0 - 24,9%.
Basal cover for individual strata was recorded as:- 0 = 0%,
1 = 1 - 2%, 2 = 3 - 4%, 3 = 5 - 6%, ...etc.

Topographic position, aspect and soil colour are multi-state variables while the others are continuous, in the sense of Sokal & Sneath (1963) and many others. Continuous variables are reduced to a limited number of states (classes) before analysis.

Equitability of sampling: comprehensive profiles and entropy of variables

The first step in Ecological profiles is the calculation of the comprehensive profile (CP) for each ecological variable. This assesses the equitability of sampling along the environmental gradient. The CP is a list of all classes of a variable with the frequency of occurrence of quadrats in each class. An example of a CP is given in Table 42 where there are a total of N quadrats.

INSERT TABLE 42

By dividing each frequency value by N, relative frequency is obtained(22).

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(22) Relative, corrected and absolute frequency are defined at length as their use in this Chapter, following the Montpellier School, differs greatly from accepted usage in America and other English-speaking countries.

If the class frequency is not too low a good estimate of the probability of occurrence may be obtained from the frequencies. If the environmental gradient has been well sampled, quadrats will be equally distributed through the classes of the CP and as a result, the probabilities of occurrence will be approximately equal. A variable for which quadrats have equal probabilities of being in each class is said to have a high indetermination (M. Godron[23] pers. comm.). Indetermination may be estimated by calculating the entropy (I_L) of variable L as:-

$$I_L = \sum_i^K \frac{R_i}{N} \log_2 \frac{N}{R_i}$$

where the symbols are explained in Table 42. Entropy is a measure of disorder (Abramson 1963). Negative entropy (negentropy of Lwoff 1965), known as information by Lance & Williams (1968), Orloci (1970) and others, is equal to entropy with the sign reversed. In this account a fundamental but inconsequent difference between entropy (used in this Chapter) and information (used in previous Chapters) is that the former uses logarithms to base two while natural logarithms are used by the latter. Entropy of

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variable L (I_L) may also be expressed in the form:-

$$I_L = \log_2 N - \frac{1}{N} \sum_{i}^{K} R_i \log_2 R_i$$

Maximum entropy ($I_{max,L}$) of variable L, which is also the highest indetermination, is found when the arithmetic mean number of quadrats occur in each class of the CP. Then:

$$R_i = \frac{N}{K} \quad \text{for all } i \quad \text{and}$$

$$I_{max,L} = \frac{K}{1} \frac{N}{K} \frac{1}{N} \log_2 \frac{N}{1} \frac{K}{N} = \log_2 K$$

In the preceding paragraphs it was shown how entropy of a variable (I_L) and maximum entropy ($I_{max,L}$) can be calculated. With these, it is possible to judge equitability of sampling. Equitability is the degree to which quadrats cover the range of variation in a habitat variable with given class intervals. The fraction (Q_L) is used to measure equitability:-

$$Q_L = \frac{I_L}{I_{max,L}}$$

Usually, the higher the value of Q, the better the sampling of total variation within the sample area. The fraction should be used with caution, however, as some variables have misleading Q values. The problem arises when variables with many classes are dealt with: for example, the 125 soil types in "Code pour le relevè" of Godron et al. (1968). Many classes will be unsampled, or very poorly represented in the CP. The value of I_{max} should, therefore, be based on the number of classes sampled adequately. If necessary, quadrats should be re-grouped into fewer classes of the ecological variable.

Equitability of species distribution: species entropy

The frequency of occurrence of species E in each class of variable L forms the ecological profile of species E for variable L. A modified ecological profile results if relative frequency or corrected frequency are used instead of absolute frequency(22) (see Gounot 1958, 1961, 1969, Godron 1965, Guillerm 1969a). The absolute frequency profile is the number of times species E occurs in each class of variable L. It gives the information for species which is given for each ecological variable by the CP. Absolute frequency may yield misleading results as it is directly proportional to the total number of occurrences. It is therefore better to use relative frequency(22) for the species ecological profile (Daget et al. 1972). If there are R_1 quadrats in a class of variable L and U_1 quadrats in that class contain species E, relative frequency is then given by:- U_1/R_1.

In order to further smooth out variations caused by differences in total absolute frequency, corrected frequency is used to form the ecological profile. Corrected frequency for class i (C_i) is

TABLE 43 Example of ecological profile for species X in K classes of variable Y.

	class 1	class 2	class 3	....	class K	Total
number of quadrats with species X	U_1	U_2	U_3	....	U_K	$\sum_{i}^{K} U_i = U_T$
number without X	V_1	V_2	V_3	....	V_K	$\sum_{i}^{K} V_i = V_T$
Total number of quadrats	R_1	R_2	R_3	....	R_K	$U_T + V_T = N$

found by multiplying relative frequency (U_1/R_1) by the inverse of average relative frequency over all quadrats:-

$$C_i = \frac{U_i}{R_i} \cdot \frac{N}{U_T} \qquad \text{(see Table 43 for explanation of symbols)}$$

INSERT TABLE 43

Information about species behaviour, which is not apparent from the absolute frequency profile, may be obtained from the corrected frequency profile.

The presence or absence of each species in an ecological profile may be used to calculate species entropy (I_s), which is defined as:-

$$I_s = \frac{U_T}{N} \log_2 \frac{N}{U_T} + \frac{V_T}{N} \log_2 \frac{N}{V_T}$$

$$\text{where} \quad U_T = \sum_i^K U_i \quad \text{and} \quad V_T = \sum_i^K V_i \quad \text{(see Table 43)}$$

A species that is either present or absent in all quadrats will have I_s equal to zero, the minimum value, and a species present in half the quadrats will have I_s equal to one, the maximum value. The relationship between relative frequency and species entropy

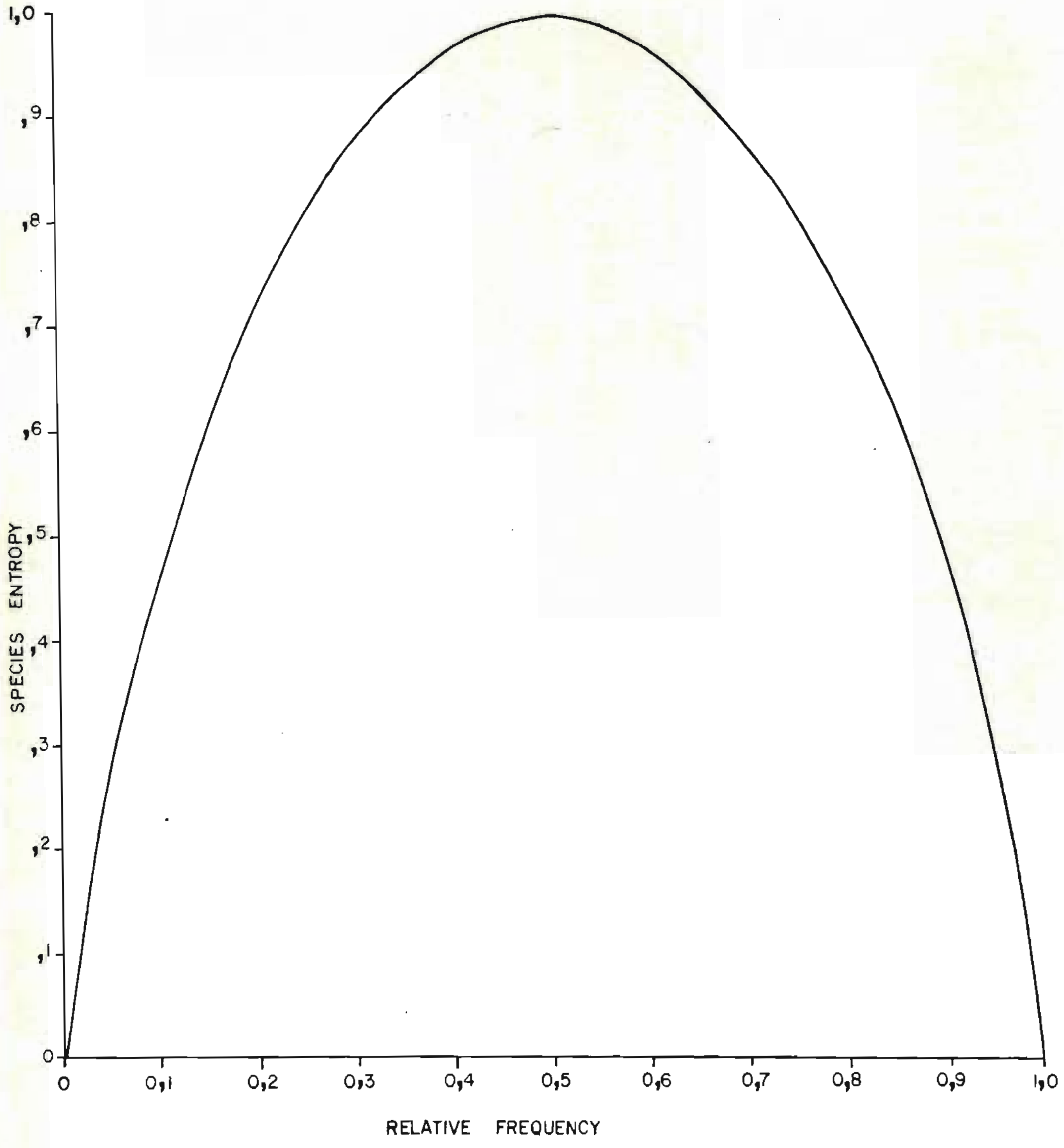

Fig. 12 Relation between species entropy
and relative frequency.

is shown graphically in Fig. 12.

INSERT FIG. 12

Mutual information between species and ecological variables

The information carried by a species relative to an environmental variable may also be calculated. It is known as the mutual information between species and variables. As mutual information may be calculated for every species with every variable, a species by variables matrix of entropy values may be produced. To reduce the volume of results, only certain species and certain ecological variables are selected, although there is no reason why all the values should not be calculated if this were required. For species E and variable L (in K classes) mutual information is given by:-

$$I_{L,E} = \sum_{i}^{K} \frac{U_i}{N} \log_2 \frac{U_i}{R_i} \cdot \frac{N}{U_T} + \sum_{i}^{K} \frac{V_i}{N} \log_2 \frac{U_i}{R_i} \cdot \frac{N}{V_T}$$

(Symbols given in Table 43)

The calculation of mutual information between species and variables allows the determination of variables that play an important rôle in the distribution of species, in other words, the 'active' variables. The most convenient way to find active variables is to calculate mean mutual information and plot the values against entropies of variables. Mean mutual information is plotted along the ordinate and entropy of the variable along the abscissa to give

TABLE 44 Comprehensive profiles for variables used in analysis. Class numbers (from Godron *et al.* 1968) do not apply to variables marked with an asterisk.

		class number										
	Variable	0	1	2	3	4	5	6	7	8	9	10
		Number of quadrats										
1.	Topographic position	13			40	19	5	2	15	11	5	
2.	Aspect	68	8		1	1	28	2		2		
3.	Slope *	69	36	5								
4.	Biotic influence		21	24	38	27						
5.	Surface rock *		16	27	41	26						
6.	Soil depth *	3	42	29	14	9	4	1	1	2	2	3
7.	Soil pH						13	57	29	11		
8.	HCl reaction	107			3							
9.	Soil colour *		33	56	5	3	3	1	3	4	1	1
10.	Total basal cover			15	68	21	6					
11.	Basal cover stratum II	9	9	10	21	43	12	5		1		
12.	Basal cover stratum IV	8	26	33	19	15	5	2		2		

a two-dimensional ordering of variables. Study of the distribution of variables within the graph allows choice of those variables which will improve sampling. On such a graph, variables placed to the right and left are respectively well-sampled and under-sampled. Variables placed at the top of the graph are more 'active' than those placed below them. To choose variables to be re-sampled, Godron (1968) suggested choosing from among those which have been insufficiently sampled (to the left of graph) and those to which the vegetation appears most sensitive (top of graph). In his application, Godron re-sampled and analysed twice to obtain a satisfactory sample.

RESULTS

Equitability of sampling

1) Comprehensive profiles of Bankenveld samples

Comprehensive profiles (CP's) for the 12 variables used in this study are given in Table 44. Inspection of the Table indicated

INSERT TABLE 44

that biotic influence, surface rock and soil pH had been fairly well sampled while aspect, soil HCl reaction and soil colour had been either inadequately sampled or class intervals had not been

TABLE 45 Observed and maximum entropy for each variable and equitability of sampling.

	Variable	Observed Entropy (I)	Maximum Entropy	Sampling equitability (Q)	Ranked Q values
1.	Topographic position	2,39	3,00	0,797	7
2.	Aspect	1,20	1,59	0,755	5
3.	Slope	1,10	1,59	0,692	3
4.	Biotic influence	1,87	2,00	0,935	12
5.	Surface rock	1,83	2,00	0,915	11
6.	Soil depth	2,05	2,59	0,792	6
7.	Soil pH	1,61	2,00	0,805	8
8.	Soil HCl reaction	0,16	1,00	0,160	1
9.	Soil colour	1,70	2,59	0,656	2
10.	Total basal cover	1,42	2,00	0,710	4
11.	Basal cover stratum II	2,31	2,81	0,822	9
12.	Basal cover stratum IV	2,27	2,59	0,876	10

well chosen. After the CP's for the 12 variables had been studied, the number of classes was reduced for five of them (see Table 41) as certain class frequencies were very low. In the case of soil depth and basal cover, adjacent classes were grouped. South, south-west, east and south-east aspects were grouped and north and north-west aspects were grouped. The two soil colour codes with high frequencies, 6/32 and 6/33 in the notation of Godron et al. (1968), were retained. In the Munsell notation these are 5YR 3/2 and 5YR 3/3, respectively, and both are named dark reddish brown. The other 6/ codes (hue 5YR) and the 7/ (hue 2,5YR), 5/ (hue 7,5YR), and 4/ (hue 10YR) codes were grouped into four classes on the basis of the 'simplified' colour wavelength code of Godron et al. While it has been suggested by M. Godron[23] (pers. comm.) that inspection of corrected frequency profiles (see Equitability of species distribution procedure) may assist in deciding which classes should be grouped, the suggestion was not acted upon in this application.

2) Entropy of variables

The observed and maximum entropy for each variable and value for Q are given in Table 45. Variables which are equitably sampled

INSERT TABLE 45

according to the Q criterion include, in decreasing order of importance, biotic influence, surface rock, basal cover for strata IV

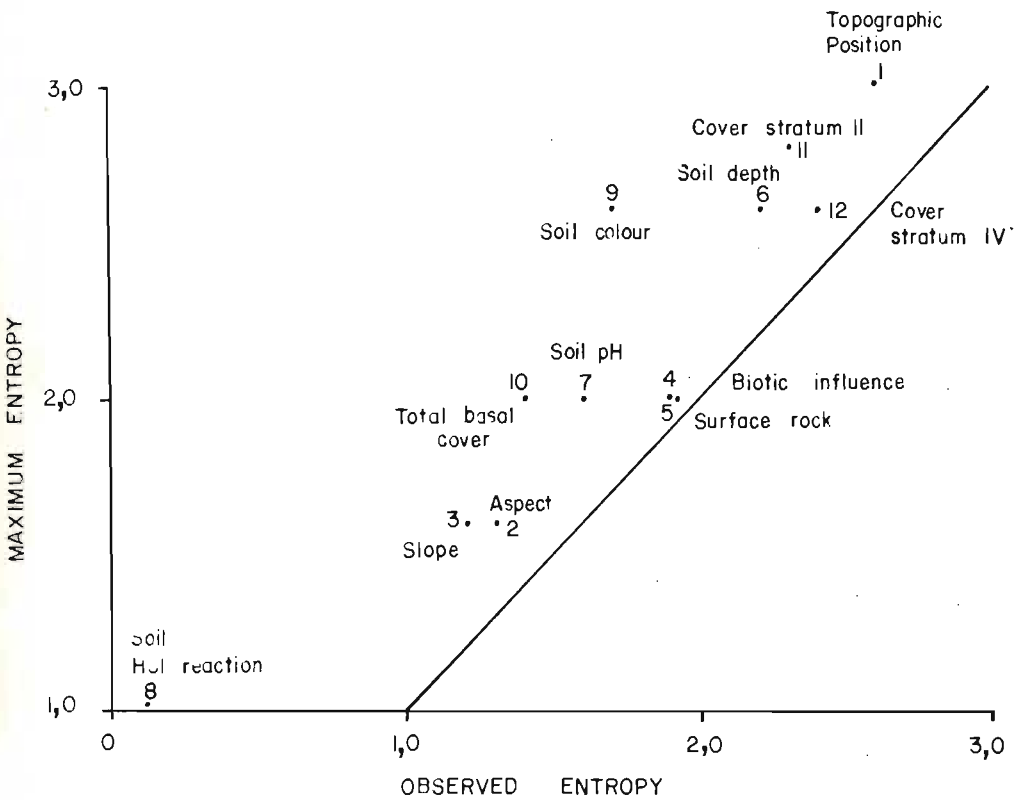

Fig. 13 Relation between observed and maximum entropy for each ecological variable. Diagonal line connects points of maximum entropy.

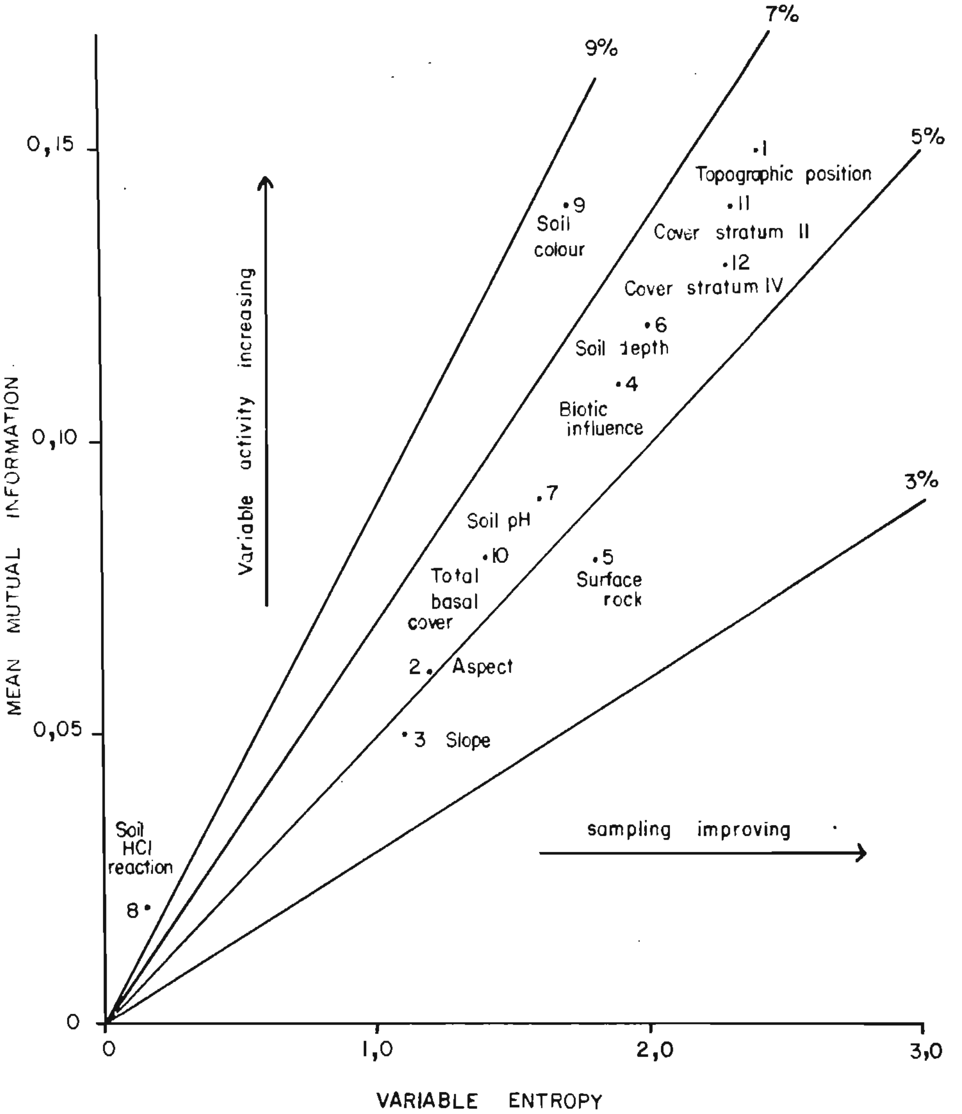

Fig. 14 Relation between mean mutual information for the species with highest information content and entropy of ecological variables.

and II, and soil pH. Observed entropy has been plotted against maximum entropy for each variable in Fig. 13. The nearer a variable

INSERT FIG. 13

is to the diagonal line, connecting points of maximum entropy, the more equitable is its sampling. Biotic influence, surface rock and cover stratum IV are most equitably sampled while soil HCl reaction, total basal cover and soil colour are, by this criterion, poorly sampled.

Mutual information between species and ecological variables

1) Overall relationships

In Fig. 14 relationships between mean mutual species information

INSERT FIG. 14

and variable entropy are given for the 12 variables. For each variable, mean mutual information was calculated over the 100 species (out of a total of 211) with highest entropies. From this graph, topographic position, cover stratum II and stratum IV, soil depth, biotic influence and surface rock are, in that order, most equitably sampled. The most active factors are topographic position, cover stratum II, soil colour, cover stratum IV, soil depth and biotic influence, in that order. With these data there

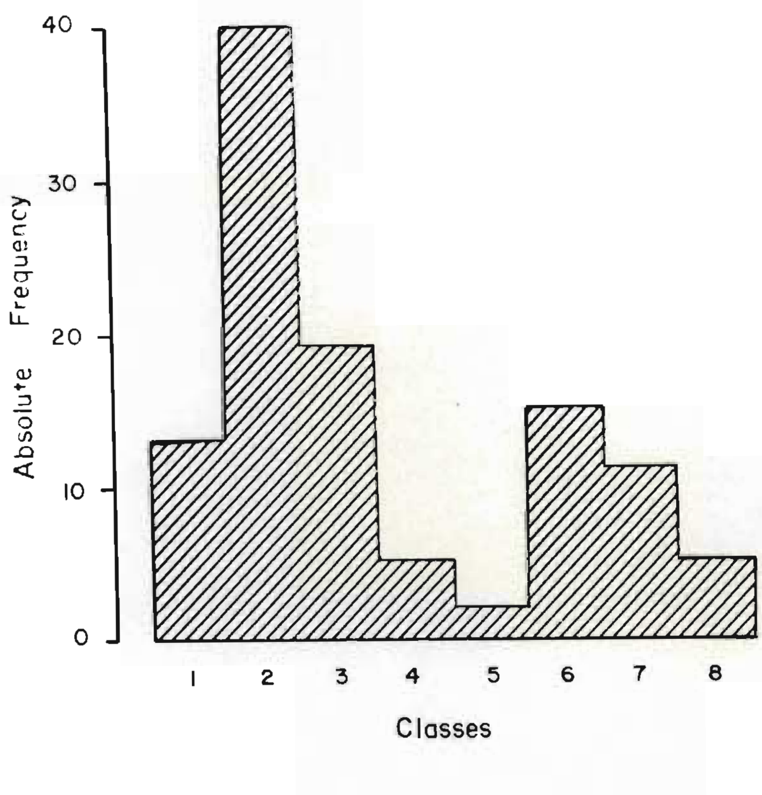

Fig. 15 Comprehensive profile (CP) for the variable topographic position (1 = flat, 2 = round summit, 3 = waxing slope, 4 = mid-slope, 5 = ledge, 6 = waning slope, 7 = open depression, 8 = closed depression).

are marked positive correlations between mean mutual information and variable entropy, illustrated by the clustering along the 5 percent line in Fig. 14. The diagonal lines in Fig. 14 give the value of mean mutual information divided by variable entropy, the fraction expressed as a percentage. It is a measure of the indicator value of variables.

In the following section, variables are discussed separately, but their relationships to each other should not be forgotten. For example, soil depth and biotic influence may be related and soil depth is often related to slope angle.

2) Ecological profiles for variables

a) Topographic position

Ecological profiles for topographic position present difficulties in interpretation although, as a variable, it is favourably placed in Fig. 14. Firstly, there is asymmetric distribution of quadrats within the classes. Class 5 is poorly sampled in comparison with other classes (see comprehensive profile, Fig. 15). Secondly,

INSERT FIG. 15

topography is a discontinuous variable, which means that a great deal of inspection is necessary to determine trends and patterns in distribution. Thirdly, the Lichtenburg area has so little relief that large differences in floristic composition related to this variable are not expected. Related to this difficulty is that of coding the variable. As coding, according to Godron et al. (1968), was done from field notes, a number of quadrats could have been misclassified. For example, the difference between an open and a closed depression, or between a flat area and the crest of a very large, rounded hill, was not always clear from field notes. It is, however, unlikely that such misclassification would materially affect the results in an ecological sense.

At the suggestion of M. Godron[23] (pers. comm.), product moment correlation coefficients were calculated by computer between each pair of corrected profiles of the 100 species with highest mean mutual information (4 950 calculations). Correlations were first calculated over all eight classes of the profile and then over the seven classes remaining after the fifth class had been excluded. As corrected frequency profiles for species over the eight classes were markedly distorted by the low CP value for class 5, the following discussion refers only to correlations over the seven remaining classes.

The 100 highest positive correlations were selected. These were all significant at $p = 0{,}01$ and the first 14 at $p = 0{,}001$. Unfortunately, these good correlations were not as satisfactory as had been expected because mean mutual information level has also to be taken into account. The following are illustrations. The highest correlation was between Dicoma anomala and Loudetia simplex that succeeded best on flat areas, rounded summits and waxing and waning slopes, according to the ecological profiles. D. anomala had the eighth highest mean mutual information value for topographic position while L. simplex was fortieth in the ranked order, indicating a low significance. Thus the profile for L. simplex is not nearly as significant as that of D. anomala, even though the profiles are highly correlated.

Gazania krebsiana, Digitaria argyrograpta and Eragrostis gummiflua profiles were highly correlated, these species being found mainly on flat areas and in open depressions according to the profiles. As all three have low mutual information values, however, the high correlations are again of little value.

With data specially collected for an Ecological profiles study, use of the correlation coefficient to compare species profiles in discontinuously-distributed variables will be desirable.

b) Aspect

Aspect was not equitably sampled and is not active in the quadrats (Fig. 14). This result was to be expected as the Lichtenburg area is very flat. In the following discussion it must be remembered that out of a total of seven classes, only three synthetic classes were retained. Species succeeding best on flat ground (no aspect) include Senecio coronatus, Gazania krebsiana and Nidorella hottentotica.

Species having competitive advantage on north and north-west aspects include[24]:-

1. Sporobolus africanus
2. Cymbopogon plurinodis
3. Eragrostis superba
4. Chascanum pinnatifidum
5. Eragrostis stapfii
6. Stipagrostis uniplumis
7. Euphorbia pseudotuberosa
8. Eragrostis lehmanniana
9. Hermannia tomentosa
10. Bulbine sp. (not collected)
11. Anthephora pubescens
12. Turbina oblongata

Species occurring most commonly on south, south-west, south-east and east aspects include:-

1. Dicoma macrocephala
2. Diheteropogon amplectens
3. Talinum arnotii
4. Coleus neochilus
5. Trachypogon spicatus
6. Blepharis angusta
7. Rhynchelytrum repens
8. Hypoxis sp. (not collected)
9. Ursinia nana
10. Menodora africana
11. Pentanisia sp. (not collected)

These lists should be considered tentative as much more intensive sampling of all aspects will be necessary to obtain a reliable picture of the influence of aspect and topographic position on species distributions.

c) Biotic influence

Results that appeared to be good were obtained from this

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(24) In the following lists, species are ordered by decreasing mutual information content. Species whose profiles are given in Figures and that are named before the lists have higher mutual information than species in the lists.

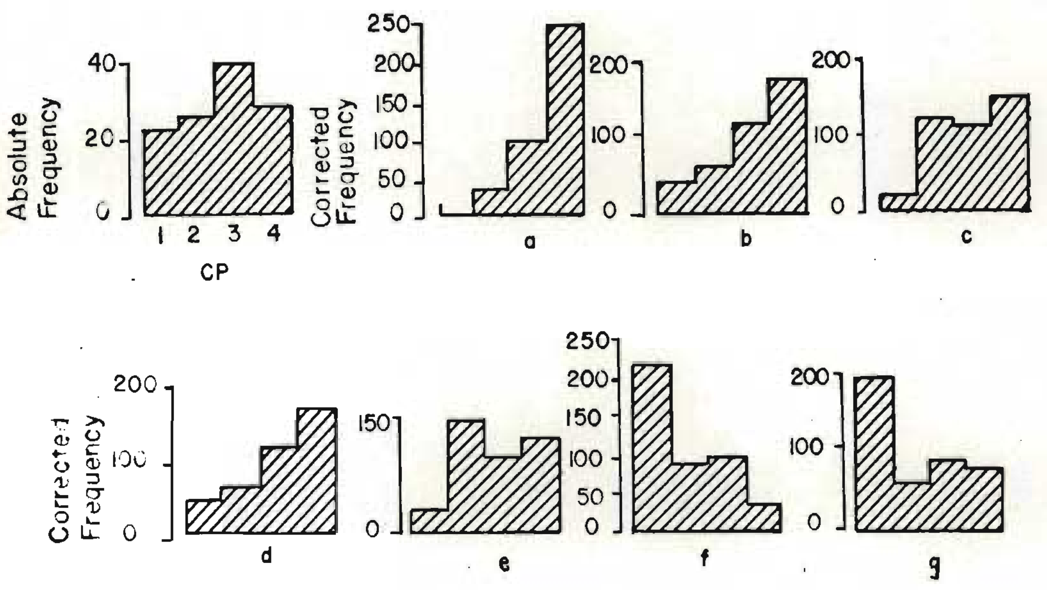

Fig. 16 Comprehensive profile (CP) and distributions of a) Cynodon dactylon, b) Eragrostis tricophora, c) Eragrostis lehmanniana, d) Ursinia nana, e) Eragrostis superba, f) Diheteropogon amplectens and g) Clematopsis scabiosifolia, representing the two main distributions within the biotic influence profile (1 = least influenced, 4 = most influenced).

environmental variable. The problem with interpreting the results was, however, that the quadrats were classed as regards biotic influence on the basis of a subjective appreciation with the result that the species composition of the quadrat influenced the assessment of the degree of biotic influence and may have distorted the ecological profiles.

As is to be expected, the main patterns of distribution along the biotic influence profile are either an increasing, or a decreasing, corrected frequency with increase in biotic influence. Good examples of increasing corrected frequency with increase in biotic influence are:- Ursinia nana, Eragrostis tricophora, Cynodon dactylon and Eragrostis lehmanniana (Fig. 16). Other species having the

INSERT FIG. 16

same trend include:-

1. Dicoma macrocephala
2. Corchorus asplenifolius
3. Blepharis integrifolia
4. Kohautia omahekensis
5. Heteropogon contortus
6. Zornea milneana
7. Euphorbia inequilatera
8. Solanum supinum

A related distribution is shown by Eragrostis superba (Fig. 16). This species as well as:-

1. Hermannia tomentosa
2. Indigofera daleoides
3. Chascanum pinnatifidum
4. Stipagrostis uniplumis
5. Eustachys mutica

are found in approximately equal proportions in the three classes of disturbed vegetation but are not common in undisturbed areas.

Species found on undisturbed areas and having successively

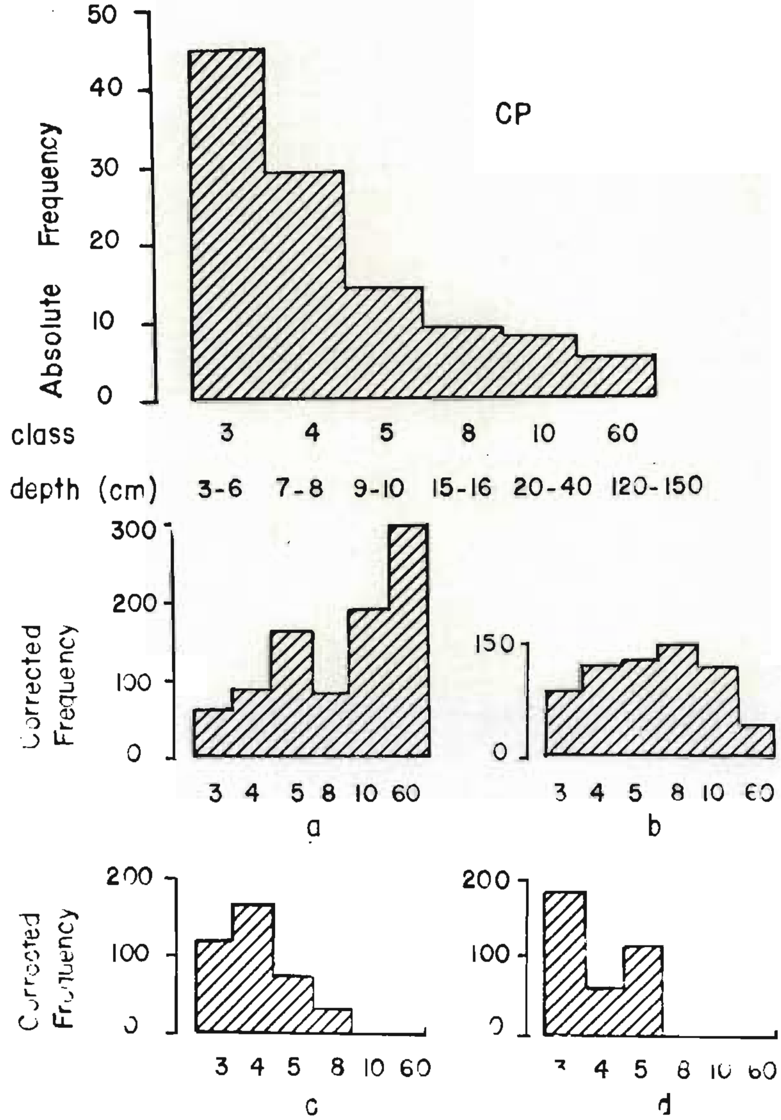

Fig. 17 Comprehensive profile (CP) and distributions of a) Zornea milneana, b) Kohautia omahekensis, c) Ipomoea obscura var. fragilis and d) Oropetium capense within the soil depth profile.

lower corrected frequencies as the degree of biotic influence increases include, notably, Clematopsis scabiosifolia and Diheteropogon amplectens (Fig. 16) as well as:-

1. Thesium costatum
2. Eragrostis racemosa
3. Schizachyrium sanguineum
4. Acalypha sp. (M&E 1267)
5. Cymbopogon excavatus
6. Heteropogon contortus
7. Barleria pretoriensis
8. Bulbostylis burchellii
9. Sporobolus pectinatus
10. Brachiaria serrata
11. Elephantorrhiza elephantina
12. Diplachne fusca
13. Senecio venosus

d) Soil depth

The comprehensive profile for soil depth (Fig. 17) shows that

INSERT FIG. 17

deeper soils (over 8 cm) were not well sampled. As the Bankenveld Land System is a dolomitic lithosol with only occasional pockets of deep soil, additional random sampling would not have improved sampling. Equitability of sampling would be achieved only with a stratified random sampling strategy whereby quadrats are placed at random within the deep-soil pockets of Willemsdal or Sterkspruit Series soils.

The ecological profile for Zornea milneana shows that it occurs on deep soil, whereas Ipomoea obscura var. fragilis and Oropetium capense are most frequently found on very shallow soil (Fig. 17). It was observed during fieldwork that the latter species

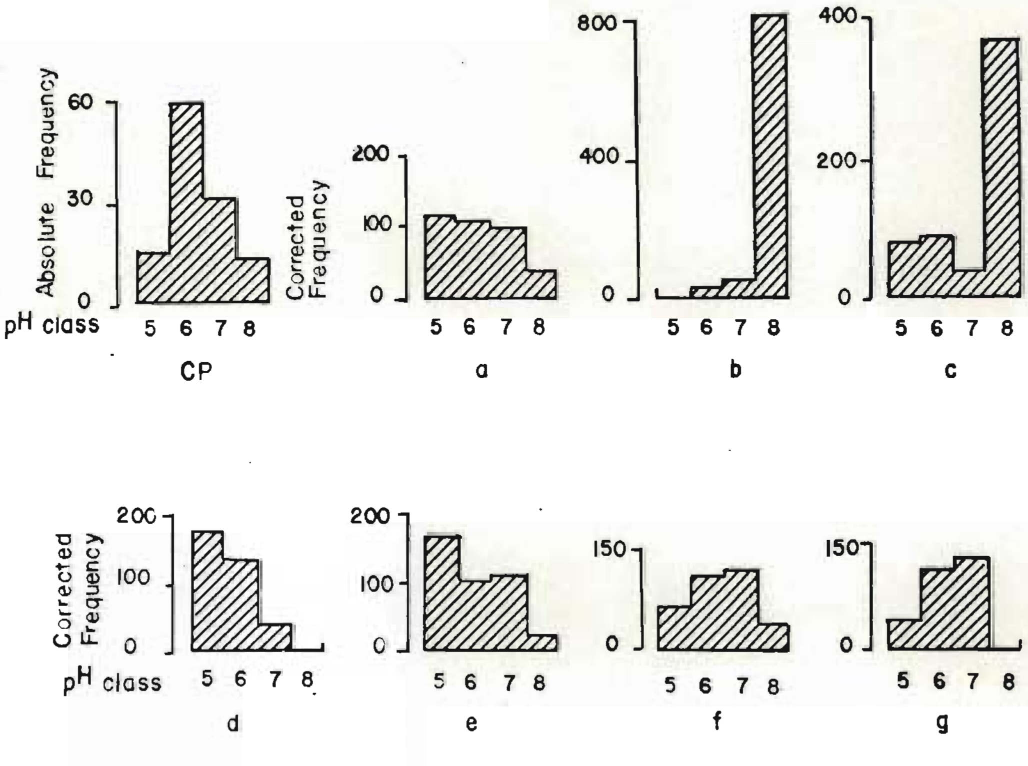

Fig. 18 Comprehensive profile (CP) and corrected ecological profiles for a) Justicia anagaloides, b) Fingerhuthia africana, c) Oropetium capense, d) Eragrostis tricophora, e) Dicoma anomala, f) Barleria macrostegia and g) Lightfootia denticulata plotted against soil pH classes.

usually occurred in small sand pockets in extensive dolomite sheets. The profile confirms the observations. Similar observations on Oropetium capense were made by Werger (1973) from the Upper Orange River Valley and by Leistner & Werger (1973) from the Kalahari. As Gaff (1971) pointed out that O. capense could withstand virtually complete desiccation, the species seems to be adapted to the extreme drought conditions of shallow sand pockets on dolomite sheets.

The profile for Kohautia omahekensis suggests that within the range included in the study it has a wide soil depth amplitude below 40 cm, but is most frequent on soils about 15 cm deep.

e) Soil pH

Although this factor was not equitably sampled (Fig. 14), valuable information about the ecology of certain species may be gained from a study of corrected ecological profiles. Certain species have been plotted in Fig. 18 to illustrate the four main

INSERT FIG. 18

trends. The most remarkable trend is shown by Fingerhuthia africana and Oropetium capense (Fig. 18), which are found only on soil with a pH of 8,0, or higher. Leistner & Werger (1973) noted that these species occurred on alkaline soils in the Kalahari. Other species showing this trend, but to a less marked extent include:-

1. Stipagrostis uniplumis
2. Turbina oblongata
3. Sporobolus africanus
4. Vernonia oligocephala
5. Brachiaria serrata
6. Euphorbia inequilatera

All these species occur on neutral and basic soils and not on acid ones.

An example of a species rarely found on soils with a pH above 7,0 is Justicia anagaloides. It grows equally well in acid or neutral soils (Fig. 18). Other species with the same distribution include Chascanum hederaceum, Eragrostis racemosa and Sporobolus pectinatus.

Species that are found on acid soils, but also grow in soil with a neutral pH include Eragrostis tricophora and Dicoma anomala (Fig. 18). Other species which exhibit this trend of decreasing corrected frequency as pH moves from acid to alkaline are:-

1. Oxygonum dregeanum
2. Pygmaeothamnus zeyheri
3. Raphionacme burkei
4. Rhynchelytrum repens
5. Hermannia betonicifolia
6. Lasiosiphon capitatus
7. Zornea milneana

Species that show a peak of corrected frequency in the centre of the range, in other words, that grow in a neutral or slightly acid soil, include Barleria macrostegia and Lightfootia denticulata (Fig. 18). Other species with similar distributions include:-

1. Helichrysum caespititium
2. Dicoma macrocephala
3. Acalypha sp. (M&E 1267)
4. Chaetacanthus costatus
5. Diheteropogon amplectens
6. Cyphocarpa angustifolia
7. Schizachyrium sanguineum

f) Basal cover

Total basal cover was inadequately sampled (Fig. 14) and is not discussed further. Within the second and fourth strata, however, three patterns of species behaviour emerged. Corrected frequencies of certain species increase as cover increases while frequencies of others decrease or, as in the third pattern, increase to a peak and then decrease again. It is stressed that cover is being used as an ecological variable and not as a structural character of the vegetation. It is assumed that amount of cover in a particular stratum influences the behaviour of certain species in the same way that soil depth and pH influence the behaviour of species.

Species for which peaks of corrected frequency are found in the centre of the profile in both the second and the fourth strata include (in alphabetical order):-

Barleria pretoriensis
Bulbostylis burchellii
Coleus neochilus
Loudetia simplex
Lightfootia denticulata
Senecio coronatus
Sporobolus pectinatus
Tephrosia longipes
Trachypogon spicatus

while species with peaks in the second stratum only include:-

1. Chaetacanthus costatus
2. Diheteropogon amplectens
3. Corchorus asplenifolius
4. Helichrysum caespititium
5. Dicoma anomala
6. Bulbine <u>sp</u>. (not collected)

and species with peaks in the fourth stratum only include:-
<u>Helichrysum cerastioides</u>, <u>Clematopsis scabiosifolia</u> and <u>Oxygonum dregeanum</u>.

Species which increase in frequency as basal cover in the second stratum increases include <u>Ursinia nana</u>, <u>Dicoma macrocephala</u>, <u>Eragrostis stapfii</u>, <u>Eustachys mutica</u> and <u>Brachiaria serrata</u> while <u>Andropogon appendiculatus</u>, <u>Diplachne fusca</u>, <u>Ipomoea obscura</u> var. <u>fragilis</u> and <u>Eragrostis racemosa</u> exhibit the opposite trend. In the fourth stratum, species which increase include <u>Thesium costatum</u>,

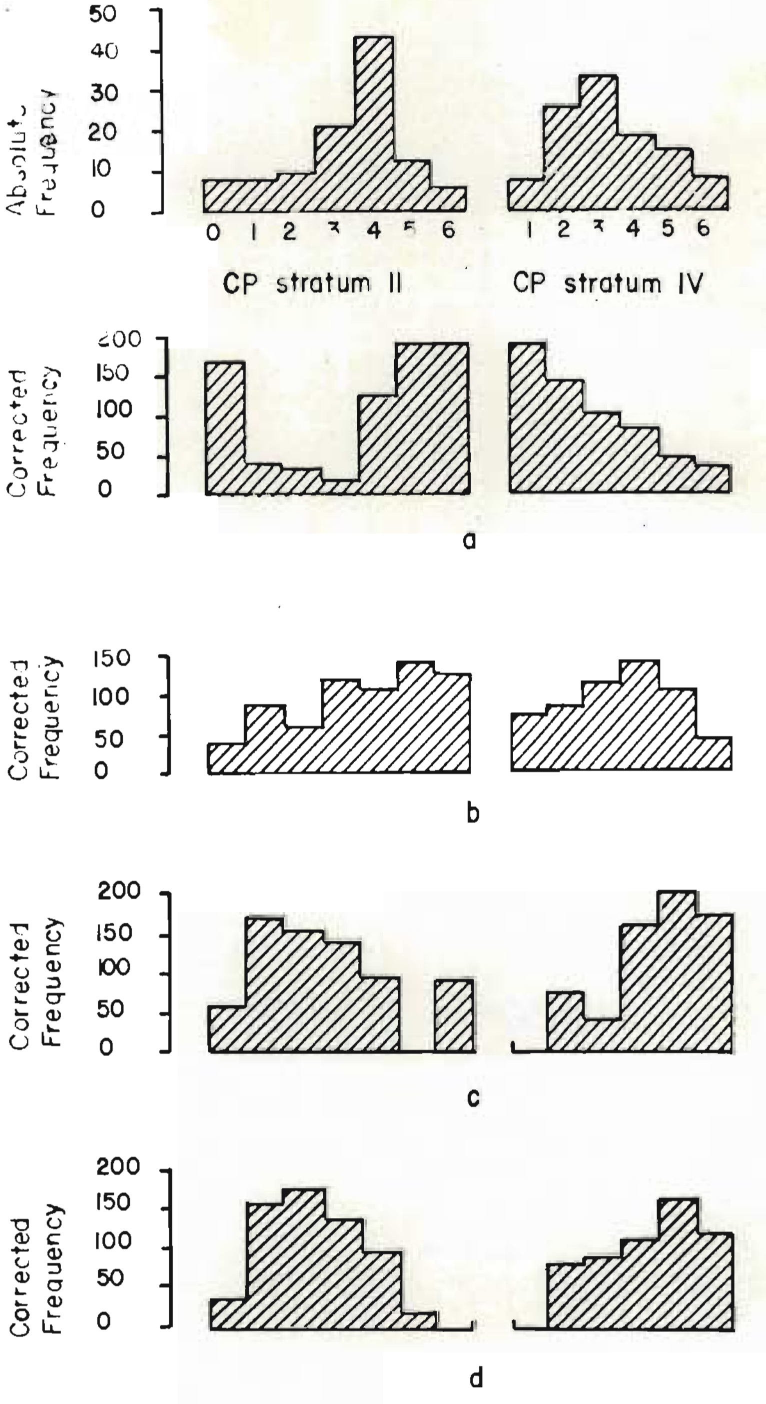

Fig. 19 Comprehensive profile (CP) and corrected ecological profiles for a) Zornea milneana, b) Acalypha sp. (M&E 1267), c) Diplachne biflora and d) Elephantorrhiza elephantina plotted against basal cover classes of the second and fourth strata.

Raphionacme hirsuta, Turbina oblongata, Pygmaeothamnus zeyheri and Nolletia ciliaris while:-

1. Blepharis integrifolia
2. Eragrostis lehmanniana
3. Setaria nigrirostris
4. Digitaria argyrograpta
5. Hibiscus microcarpus
6. Cynodon dactylon
7. Lippia scaberrima
8. Mariscus capensis
9. Sida chrysantha

decrease in corrected frequency as basal cover in the fourth stratum increases.

In addition to the three expected trends described above, certain species had unexpected distributions when both strata were taken into account. These are illustrated in Fig. 19. Diagrams

INSERT FIG. 19

such as these could have been drawn for all the species listed but where the pattern of distribution was clear this was not thought necessary. Zornea milneana, a short, creeping herb shows a marked U-shaped curve in the second stratum and decreases sharply in the fourth stratum as basal cover in both strata increases. Acalypha sp. (M&E 1267), another short herb, increases in frequency in the second stratum as cover increases but reaches a peak in the fourth class of the fourth stratum. Species which decrease as cover in the second stratum increases and increase as cover in the fourth stratum increases are Diplachne biflora and Elephantorrhiza elephantina.

Although basal cover in both strata II and IV are active and well-sampled variables (Fig. 14), inspection of the comprehensive profiles (Fig. 19) shows that the distribution of quadrats through the classes is far from regular, which may account for the odd patterns described above. Although the patterns are clear the differences in corrected frequency through the profiles are often smaller than with some of the variables already described.

g) Other variables

Other variables are not discussed in detail. The variable, surface rock, is closely correlated with soil depth in this study and ecological profiles of each are similar. As slopes within the study area were so gentle, if present at all, the slope profile does not carry much information. HCl reaction was poorly sampled and trying to attach ecological significance to soil colour in this study area was not considered worthwhile as differences in soil drainage, causing differences in soil colour, were not apparent.

DISCUSSION

Sampling considerations

For ecological profiles it is necessary to calculate the entropy of species, ecological variables and mutually between species and variables. The calculations assume the frequency distribution to be related to the probabilities of species occurrence. The collection of quadrats is considered as a "population" and is treated as such. This equivalence has its limitations in that it assumes that the number of quadrats is "large". By the use of a more complex formula it is possible, however, to overcome this drawback and use relatively "small" samples. Experience from analyses at Montpellier shows that, with the formulae described in this Chapter, about 100 samples are necessary for a reasonable first approximation. With fewer quadrats the results should be used only as a guide although the conclusions regarding the necessary improvements to sampling are always useful.

Montpellier ecologists (Daget et al. 1972) stress that the main application of the Ecological profiles technique is sampling improvement. The best approach in the use of this technique for sampling improvement will be to record about 100 quadrats and then carry out a first Ecological profiles analysis. Sampling deficiencies will show up clearly, as, for example, soil HCl reaction in this application (Figs 13 & 14). The study area can then be stratified in such a way that sampling is biased towards under-sampled variables but retains its random element. After, say, another 50 quadrats, profiles can be calculated again and sampling deficiencies can again be sought. The cycle of re-sampling and re-analysing can be continued until the user is satisfied with the sampling. It should be borne in mind that one should first start improving the sampling of variables considered important in the study. It may happen that it will be virtually impossible to improve the sampling of a certain variable because of the nature of the study area (only one class of a variable represented in the area). In the present study it was not possible to re-sample the vegetation and therefore some profiles were unsuitable for providing information for an ecological

TABLE 46 Species ranked in one of the first 20 positions for at least four variables and the variables for which they were so ranked. Names of variables corresponding to numbers are given in Table 47.

species	variable number 1	2	3	4	5	6	7	8	9	10	11	12	Total
1. Stipagrostis uniplumis	*	*	*		*	*	*		*	*		*	9
2. Schizachyrium sanguineum	*	*	*	*		*			*		*		7
3. Turbina oblongata				*	*	*	*	*	*	*			7
4. Dicoma macrocephala		*		*	*		*				*	*	6
5. Justicia anagaloides				*	*		*	*	*		*		6
6. Diheteropogon amplectens		*	*	*					*			*	5
7. Brachiaria serrata			*				*	*		*		*	5
8. Cymbopogon plurinodis		*	*		*				*	*			5
9. Dicoma anomala	*		*	*			*		*				5
10. Eragrostis lehmanniana			*				*	*		*	*		5
11. Eragrostis superba		*	*	*	*				*				5
12. Indigofera daleiodes	*			*		*					*	*	5
13. Ipomoea obscura v.fragilis	*				*	*		*		*			5
14. Oropetium capense					*	*	*	*			*		5
15. Eragrostis curvula			*	*	*							*	4
16. Eragrostis racemosa				*			*			*		*	4
17. Eragrostis stapfii		*			*	*				*			4
18. Fingerhuthia africana					*		*	*	*				4
19. Loudetia simplex				*						*	*	*	4
20. Oyphrestia retusa	*	*	*						*				4
21. Senecio coronatus		*	*	*		*							4
22. Senecio venosus	*	*	*			*							4
23. Sporobolus africanus		*	*			*	*						4
24. Thesium costatum	*			*	*							*	4
25. Ursinia nana	*			*							*	*	4

interpretation of species-habitat relationships.

The ecological profiles technique is applicable in homogeneous study areas. There was probably too much variation even within the 110 Bankenveld samples for conclusive results to be expected. The technique will probably work best at the detailed level of survey of small areas (mapping scales larger than 1:50 000). The crossing of marked ecological boundaries within the same analysis (e.g. Bankenveld and CT Grassland Land Systems) should be avoided.

Species indicator values

For every ecological variable, species may be ranked by decreasing mutual information content. The position of a species in the list is then what is known in France as the indicator value of the species for the variable. The species with highest mutual information content has the highest indicator value for that variable. While study of the corrected ecological profiles allows specification of the ecology of a species, it is possible to identify the species whose ecological requirements are most similar by means of these indicator values.

Species with the 20 highest indicator values for each of the 12 variables were listed and those species which were included on lists of four or more variables are given in Table 46. In particular,

INSERT TABLE 46

Stipagrostis uniplumis, *Schizachyrium sanguineum* and *Turbina oblongata*

TABLE 47 Mutual information between five species and 12 variables ($\bar{x}$ = mean mutual information, 1 = Stipagrostis uniplumis, 2 = Schizachyrium sanguineum, 3 = Turbina oblongata, 4 = Dicoma macrocephala, 5 = Justicia anagaloides).

	Variable	$\bar{x}$ for first 100 species	species number 1	2	3	4	5
1.	Topographic position	0,145	0,169	0,174	0,152	0,142	0,121
2.	Aspect	0,060	0,097	0,109	0,050	0,098	0,039
3.	Slope	0,053	0,068	0,071	0,047	0,045	0,045
4.	Biotic influence	0,110	0,133	0,155	0,142	0,208	0,144
5.	Surface rock	0,084	0,112	0,095	0,121	0,104	0,113
6.	Soil depth	0,121	0,171	0,161	0,157	0,116	0,112
7.	Soil pH	0,093	0,128	0,095	0,124	0,124	0,158
8.	HCl reaction	0,024	0,028	0,012	0,043	0,012	0,063
9.	Soil colour	0,138	0,335	0,197	0,298	0,113	0,206
10.	Basal cover	0,075	0,098	0,062	0,094	0,081	*
11.	Basal cover stratum II	0,139	0,162	0,172	0,128	0,174	0,168
12.	Basal cover stratum IV	0,129	0,151	0,145	0,137	0,245	0,123

* not calculated

have high indicator values for many variables (Table 46). Most species are active in variables 3 (slope), 4 (biotic influence) and 5 (surface rock) and fewest in 8 (HCl reaction) and 11 (cover stratum II).

Instead of looking at the species by variables matrix of mutual information, one ecological variable at a time, as was done here, it may be studied species by species over all variables. In Table 47, mutual information values for five species are given for

INSERT TABLE 47

the twelve ecological variables. The five species occurred in one of the first 20 ranked positions of more than five variables. To obtain a point of reference for each variable, the mean mutual information for the 100 species with highest mutual information values is given for each variable. By comparing the mean mutual information value with individual values the relative importance of each species may be obtained. Thus, for the variable, topographic position, Schizachyrium sanguineum is most important with a mutual information content of 0,174. As Stipagrostis uniplumis and Turbina oblongata also have mutual information values that are higher than the mean (0,145), it can be assumed that they are also important species. Justicia anagaloides is least important with a mutual information content of 0,121. Any species in which one is interested can be studied in this way, but for detailed study, it will be necessary to use either the species rank or, at least, a corrected value as reference point in place of the actual mutual information value. Comparison between variables will otherwise be difficult, if not impossible.

Indicator groups

According to Daget et al. (1972), species with similar ecological profiles and carrying a high information content for the same variables form 'ecological groups'. To avoid confusion with 'ecological groups' in the community sense, M. Godron[23] (pers. comm.) suggested the term 'indicator group' for these species. An indicator group is, then, a collection of species with the same, or similar, ecological requirements. From past work, according to Daget et al., it appears that the number of groups of species or of isolated species stabilises rapidly. The succeeding groups confirm those that have been established before or only modify them slightly. As many ecological variables are usually correlated (for example, slope angle and soil depth in this study) and the active variables are analysed first, the remaining variables usually add little new information. Any number of indicator groups may be established for a variable as the distribution of species along a continuous environmental gradient is continuous, or nearly so. The species may be ordered in a series of groups that are scale-imbricated. Ordering may be done automatically with the aid of a card sorter (Daget & David 1970).

In this study, species that had the same, or a similar pattern of response to a variable were discussed together (see Results: ecological profiles for variables) but no attempt was made to derive indicator groups as the data were considered incomplete.

CONCLUSION

Ecological profiles is a graphic technique. The theory is not difficult to understand and results are fairly easy to interpret. Specially-collected data are not necessary, but desirable, as evidenced by the use of association analysis data in this account.

As it is univariate, it may be difficult to separate the influences of related, or strongly correlated ecological variables. In this account, soil depth and angle of slope produced similar profiles as they were correlated variables. Information on correlation between variables cannot be derived from the analysis directly as, for example, it can from a principal components analysis of habitat variables.

The most difficult problem in using the ecological profiles technique is the erection of class intervals for continuously distributed variables. Results depend, to a large extent, on these decisions, which have been subjective in the past. It is suggested that, for consistency, the "Code pour le relevé" of Godron et al. (1968) be followed. Use of one's own class intervals (and variables, for that matter) is possible, but subjective judgment then becomes critical and the standardization of field observations called for by Godron & Poissonet (1970) to aid comparison between surveys is, of course, no longer possible.

With adequate sampling of ecological variables, determination of the ecological profiles of common South African plant species for the most important environmental variables would provide the kind of information needed to explain the ecology of South African vegetation and hence its rational management and use. As a species may behave differently in different parts of the country and ecological profiles are most applicable to fairly small, homogeneous areas a number of profile studies will be necessary for each species and each environmental variable. Because of inadequate sampling, the ecological results of the Lichtenburg analysis should be treated with caution. They indicate, however, the great potential value of the technique.

CHAPTER 7

GENERAL DISCUSSION AND CONCLUSIONS

Specific conclusions are given, as appropriate, at the ends of other Chapters in this account. In this Chapter, some thoughts on the future of automatic classification and ecological profiles in South Africa are outlined in the light of experience gained through this and other quantitative ecological studies. As the sampling strategy should be an integral part of the whole in all ecological surveys it is also discussed briefly.

FUTURE SAMPLING STRATEGIES

The stratified-random sampling strategy used for the present survey was both efficient and sufficient. It was efficient in covering the variation adequately and sufficient in that a limited number of samples provided acceptable results. One possible improvement, derived from the Braun-Blanquet School's sampling strategy (Werger 1973) would be the choice of a representative sample at the site indicated by inspection of the aerial photograph in the field to be the sample site, instead of selecting a site by throwing a marked metal stake in a random manner as done in this study. Werger (1973) discusses the concept of a representative sample and the subject is not broached here except to state that the sample selected should be representative of the vegetation type delimited on the aerial photograph before going into the field. Choice of sample sites in this way should reduce 'noise' in the data and yet retain sufficient objectivity for automatic classification techniques.

Quadrats of 16 m^2 appeared from the technique studies to be sufficiently large for the herbaceous stratum of the vegetation. It was also apparent that reduction in quadrat size had very little effect except in cases of extreme data reduction so that quadrats of 12 to 16 m^2 would seem adequate for grassland of this type. Classifications based on the first few species recorded in every quadrat were satisfactory in the present study, where the full species complement was actually recorded in the field. Such a strategy has little in its favour for future surveys excepting speed, however, as in applying it one may subconsciously look first for the species one expected to be in the quadrat or for species one knew. It also means that fewer more common species will be recorded, leading to less adequate characterisation by presence percentages of automatic classification final groups.

Habitat data recorded from quadrats should be as good as possible, both for interpretation of floristic classifications and also for multivariate analysis of habitat data. A rule-of-thumb might be to spend approximately the same time at each quadrat on habitat data as on floristic data. Abbreviated data in this study hampered interpretation and severely handicapped the use of Ecological profiles.

Finally, in connection with the sampling strategy, it is considered that less surveying effort should have been expended on the CT Grassland Land System. At the semi-detailed scale of the present survey it would have been better to either ignore the extensively-ploughed CT Grassland Land System as a whole or to have concentrated efforts only on those plant communities which were less extensively ploughed, even though they cover a relatively small proportion of the whole study area. By restricting samples in this way, more information could have been extracted about communities that are important from the point of view of the natural and semi-natural vegetation of CT Grassland.

AUTOMATIC CLASSIFICATION

The nature of vegetation is probably such that an automatic method of classification will never be able to provide a perfect classification. Refinement, in the form of re-allocation of quadrats will usually be either necessary or desirable. Re-allocation, or final sorting, should be based on habitat information and species from the surround of samples as done in this study. Use of the total floristic complement (presence and abundance) of the quadrats, as done by the Braun-Blanquet School, would be a desirable further sophistication of the classification technique.

It is currently considered that the Braun-Blanquet technique (BB) is a generally more rapid method of semi-detailed survey than association analysis and other automatic techniques. There is probably no real difference in speed, which, in both cases, is dependent upon the individual ecologist responsible for the survey and the level of detail required. Both BB and automatic techniques require training and experience before acceptable results are forthcoming. Although association analysis is 'automatic', it cannot be used by untrained technicians and the same holds for BB techniques.

Experience is also needed for the interpretation of the hierarchies produced from automatic classifications. The raw hierarchy is not a one-dimensional ordination where gradients in environmental factors should be expected from left to right and vice versa. In general terms, the more nodes that separate groups, the more different the groups are. In the present study, however, more than one pair of groups which were widely separated on the hierarchy were shown to be closely related ecologically. The computer division could be explained in most instances: usually, in terms of management differences. An automatic classification hierarchy is not meant to be interpreted in the hierarchical manner of the Braun-Blanquet school.

Even if it is conceeded that the straight-forward use of association analysis, or some related technique, without re-allocation and other refinements will usually provide an answer that is too crude for acceptance, the need for an initial, preliminary sort of samples into even rather vague groups is necessary. The writer considers that an automatic classification might be preferable to the first sort of a BB association table for this purpose. Only if the ecologist is extremely familiar with the area and the vegetation under study and if there are marked differences within the vegetation will BB not create problems at this stage in synthesis. An initial BB sort will be particularly inefficient in vegetation like fynbos (macchia) where Boucher (1972) failed to extract meaningful groups. Automatic classification can provide a quick, objective initial sort of the samples into groups which may then be refined by the BB method.

ECOLOGICAL PROFILES AND ORDINATION

The Ecological profiles technique was found useful for the correlation of species behaviour with habitat conditions. Although not done in the present study, Ecological profiles can be used for improvement of sampling as well. It could form a logical extension to the sampling strategy discussed above. It can also be used to elucidate automatic classification results, or BB results for that matter, although a multivariate ordination technique may be preferable in certain instances as Ecological profiles is not suitable for the study of direct correlation between habitat variables.

A body of evidence is presently being built up, particularly through the work of O.J.H. Bosch[25] and J.E. Granger[26], showing that principal components analysis (PCA) does not perform as poorly on real data as made out by Gauch & Whittaker (1972), after a study using simulated data. Even though PCA may also have the theoretical limitations described by Beals (1973), it and Factor analysis of correspondences (Romane et al. 1973) are probably still the best ordination techniques for the study of direct correlation between habitat variables. Once again, the conclusion is that sensible use of all ecological techniques is called for.

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S U M M A R Y

A quantitative, semi-detailed plant ecological study of the area between 25° 54' and 26° 22' E and 26° 00' and 26° 20' S, situated around the town of Lichtenburg in the South-western Transvaal, is reported.

The average daily maximum temperature of the study area is about 28 °C in January and 18 °C in July but extreme daily maxima of 37 °C (January) and 25 °C (July) have been recorded. Average daily minima range from about 15 °C in January to 2 °C in July while extreme minima of 6 °C (January) and -10 °C (July) have been recorded. The period during which frost is likely to occur lasts, on average, for 106 days from May to September with frost actually being recorded on about 26 days. Mean annual precipitation is about 600 mm, due almost exclusively to showers and thunderstorms. Winter months are normally dry and about 85 percent of the annual precipitation falls during the summer months from October to March. On an average hail occurs four to seven times annually.

The study area lies between 1460 and 1520 m above sea level and consists of a large, undulating plain characterised by the absence of marked topographic features. When all physiographic features are taken into account two Land Systems are apparent. The Bankenveld Land System is underlain by dolomite, variously covered by alluvial gravels on the Karst structural phase of the African erosion surface and having lithosolic soils. The Veld Type is Bankenveld and cattle ranching is the chief land-use.

The CT Grassland Land System is underlain by granite, Ventersdorp lavas, Dwyka tillite and surface limestone on the aggradational phase (aeolian sand) of the African erosion surface. Soils of Shorrocks, Mangano and Lichtenburg series are generally sandy and well-drained. The natural vegetation is Dry Cymbopogon-Themeda Veld or Sandy Cymbopogon-Themeda Veld, but most of it has been destroyed by cultivation of maize, the chief land-use.

A stratified-random sampling strategy, using aerial photographs was used to place 110 quadrats within each Land System. The basic 4 by 4 m quadrat was divided into four triangles by lines connecting diagonally opposite corners of the square. Nested samples of 4, 8, 12 and 16 m^2 were thus available by successive addition of triangles. Species present in a strip,about two metres wide, round the perimeter of the quadrat were also recorded. Physical factors recorded for each quadrat included geology, geomorphology, aspect, angle of slope and exposure. Soil series and depth were recorded and for each soil horizon, soil pH, reaction to dilute hydrochloric acid, moist Munsell soil colour and soil texture were noted. Biotic influence was also noted. Total basal cover and the height and basal cover of each constituent stratum were estimated for the 16 m^2 quadrat. The presence of all permanently recognisable plant species and their cover-abundance estimate were recorded. The order in which species were encountered was noted, as were additional species found with each increase in sample size.

The monothetic-divisive technique of association analysis was used for classification of the quadrats. An association analysis (known as the Total analysis) was carried out on the 220 quadrats (16 m^2) of the study area and then another (known as the Bankenveld analysis) was carried out on the subset of 110 quadrats of the Bankenveld Land System. The former was to obtain an overall classification of the vegetation of the area and, in particular, to enable definition of the main plant communities. The second analysis was to obtain in-depth information about Bankenveld, the area whose natural and semi-natural vegetation was of most importance. For both analyses, species occurring in fewer than six quadrats were masked.

A map of the vegetation of the study area was drawn at a scale of 1:50 000 and a check list of plants collected was made.

Inspection of final groups derived from the analysis suggested that on the bases of their habitat data being markedly dissimilar from those of other quadrats of the group, certain quadrats were misclassified. By reference to species listed from the area surrounding each misclassified quadrat, they were re-allocated to another group on the basis of the dividing species of the hierarchy.

A total of 247 species were encountered in the study area. Within the Bankenveld Land System, 211 species were encountered and 165 were found in CT Grassland quadrats. Most of the species had low overall frequencies. In the whole area nearly 100 species occurred in less than six quadrats. A few species, including Themeda triandra Aristida congesta, Elionurus argenteus, Anthospermum rigidum and Justicia anagaloides were common throughout the study area.

The largest number of species in a quadrat (16 m^2) was 54, recorded from a Bankenveld Land System quadrat. The lowest number of species was 11 in a CT Grassland quadrat. The overall average was 30,4 with a standard deviation of 9,0.

The Total association analysis did not completely separate Bankenveld Land System quadrats from CT Grassland quadrats. Of the four major groups of the hierarchy the first two were largely of Bankenveld and the last two mainly of CT Grassland quadrats. Bankenveld groups of the Total analysis were not interpreted. Eleven final groups were recognised and described from the CT Grassland part of the Total analysis.

Two final groups, Short and Tall Stipagrostis uniplumis Calcareous Grassland, occur on soils overlying surface limestone deposits. The communities are found around Lichtenburg and in a belt to the west of the town. Species common in one or both Groups include:- Stipagrostis uniplumis, Aristida congesta, Brachiaria serrata, Themeda triandra and Vernonia oligocephala.

Another two final groups, Elionurus argenteus Secondary Grassland and E. argenteus Primary Grassland occur on rocks of the Ventersdorp System. Most of these communities are found south-west of Lichtenburg. Species common in one or both Groups include:- Elionurus argenteus, Anthospermum rigidum, Aristida congesta, Brachiaria serrata, Eragrostis curvula, Heteropogon contortus, Themeda triandra and Setaria flabellata.

Two final groups occur on Dwyka tillite substrate. They are Cymbopogon plurinodis Grassland and Secondary C. plurinodis Grassland. Species common in one or both Groups include:-

Cymbopogon plurinodis, Barleria macrostegia, Blepharis integrifolia, Elionurus argenteus, Eragrostis curvula, Eustachys mutica, Hermannia depressa, Themeda triandra and Triraphis andropogonoides.

Three final groups, Acacia karroo Savanna, A. karroo Open Woodland and Drainage Basin A. karroo Open Woodland are found on the medium- to poorly-drained soils of the area along the Harts River. In all three groups a woody element is present with Acacia karroo as the dominant tree and shrub species. Other species commonly found in one or more of these Groups are:- Aristida congesta, Barleria macrostegia, Blepharis integrifolia, Cynodon dactylon, Digitaria argyrograpta, Eragrostis curvula, Felicia muricata, Lippia scaberrima and Sporobolus africanus.

Two final groups are neither named nor mapped as it was found that they were not homogeneous and that their quadrats occurred scattered through the study area.

It was concluded that the major vegetational differences in CT Grassland could be related to the geological substrate and gross soil characteristics. Within major groups, management was an important factor.

Seven major groups were distinguished in the Bankenveld association analysis. Group 1 (Diheteropogon-Stipagrostis Primary Bankenveld) consists of quadrats laid out in vegetation that is well managed. Group 2 (Diheteropogon-Schizachyrium Bankenveld), actually consisting of four final groups, is considered to be the typical vegetation of the Bankenveld Land System. Species common in Group 1 include:- Diheteropogon amplectens, Stipagrostis uniplumis, Anthospermum rigidum, Brachiaria serrata, Crabbea angustifolia and Euphorbia inequilatera. Species common in Group 2 include:- Diheteropogon amplectens, Schizachyrium sanguineum and Aristida diffusa var. burkei. It was found that many species were common to all, or most, of the groups and that very few species were common in only one or two final groups.

Quadrats of Groups 3 and 4 (Chascanum-Eragrostis racemosa Sandy Bankenveld and Chascanum-Anthephora pubescens Sandy Bankenveld) occur together on the western edge of the Land System and in a circular patch in the north-west of the study area. Both groups are found where sand overlies dolomite. Common species include:- Chascanum hederaceum, Eragrostis racemosa, Anthephora pubescens, Aristida congesta, Justicia anagaloides and Themeda triandra.

Quadrats of Group 5 (Corchorus-Ursinia Bankenveld of Disturbed Sites) are laid out in vegetation that had been disturbed in the past. Common species include:- Corchorus asplenifolius and Ursinia nana.

Group 6 (Fingerhuthia-Oropetium Bankenveld of Dolomite Sheets) quadrats are characteristic of exposed sheets of dolomite, found particularly in the area to the immediate north of Lichtenburg. Common species include:- Fingerhuthia africana, Oropetium capense, Aristida congesta, Stipagrostis uniplumis and Turbina oblongata.

Group 7, the last group of the analysis, is neither named nor mapped.

As part of a technique study, the 110 Bankenveld Land System quadrats were classified by means of divisive information analysis

(DIVINF) and axis ordination (AXOR) and results compared with those of the association analysis. All three classifications produced results which were basically very similar. It was found that association analysis was sensitive to the number of species recorded in each quadrat while the other two techniques were not.

Various methods of data reduction, including reduction of quadrat size to 8 and 4 m^2, using only the first 19 and first 12 species recorded in each quadrat and masking species in 10 or fewer quadrats, were applied to the Bankenveld Land System quadrats. DIVINF and association analysis were used to classify the reduced data and by means of two objective methods for comparing groups and two methods for comparing groups and configurations of the hierarchies, it was found that remarkably similar results were obtained even with severe data reduction. It was concluded that objective methods were of use for comparing the results of classifications but that an in-depth study at every hierarchical level was necessary. A new comparison technique which considers group constitution and group configuration simultaneously at all hierarchical levels is necessary. It was also concluded from this technique study that data reduction, as a means of saving computer time, can be justified.

The Ecological profiles technique was applied to the Bankenveld Land System data after the technique had been described in detail, for the first time in English. Although the data were inadequate, results showed the utility of the technique. It was concluded that with adequate sampling of ecological variables, those having the greatest influence on the distributions of species would be revealed, thereby providing the kind of information needed to explain the ecology of South African plant species and hence their rational management and use.

It is finally suggested that in future a slightly modified sampling strategy should be used for semi-detailed surveys. The stratified-random approach used for this study should be retained except that the actual position of the quadrat at the sample site should be chosen instead of being left to chance.

Even if it is concluded that the straight-forward use of association analysis, or another method of automatic classification, without subjective re-allocation and other refinements will usually provide an answer that is too crude, such automatic classification can at least provide the necessary, preliminary sorting of quadrats to be refined by a technique like that of the Braun-Blanquet School.

APPENDICES

CLIMATOLOGICAL TABLES A1 TO A14

TABLE A1 Monthly march of radiation at Pretoria in cal/ cm^2 /day.

	Global radiation means of daily sums (G) *	Diffuse radiation means of daily sums (D) *	Direct radiation means of daily sums (G-D) *	Maximum total radiation recorded on single day **	Minimum total radiation recorded on single day **
January	585	201	384	800	123
February	531	191	340	778	127
March	486	161	325	687	130
April	418	113	305	575	57
May	366	79	287	486	58
June	341	69	272	420	47
July	358	75	283	437	27
August	437	87	350	561	122
September	500	113	387	649	30
October	544	158	386	727	79
November	559	185	374	792	151
December	566	200	366	797	138
Year	474	136	338	800	27

* From Weather Bureau (1968), period 1951-1962

** From Schulze (1965), period 1951-1959

TABLE A2 Monthly means of hourly sums of global (G) and diffuse (D) radiation in cal/cm^2/hour at Pretoria for the period 1951 - 1962 from Weather Bureau (1968).

hour ending	January		March		May		July		September		November		Year	
	G	D	G	D	G	D	G	D	G	D	G	D	G	D
0600	2,6	1,5	0,2	0,1	0,0	0,0	0,0	0,0	0,0	0,0	1,8	1,1	0,8	0,5
0700	14,9	6,1	7,3	3,5	1,1	0,5	0,7	0,3	5,4	2,3	12,6	5,6	7,0	3,1
0800	30,8	11,1	22,2	8,0	11,3	3,4	10,2	3,4	21,1	6,3	27,6	10,4	20,5	7,1
0900	46,0	16,0	38,9	12,7	27,0	6,1	25,7	6,0	38,1	9,4	47,9	14,5	36,3	10,8
1000	59,9	20,3	52,6	16,3	40,3	8,4	39,4	8,0	53,5	11,9	57,9	18,2	50,3	13,8
1100	69,7	22,3	62,9	18,7	50,1	9,9	49,4	9,4	64,7	13,2	67,4	21,3	60,6	15,8
1200	74,6	23,4	66,9	20,7	54,9	10,4	54,9	10,2	69,9	13,6	72,1	22,3	65,6	16,8
1300	73,6	23,5	66,1	20,4	55,2	10,3	54,7	10,1	69,4	13,7	72,9	21,9	65,1	16,7
1400	68,5	21,9	59,1	19,1	49,5	9,9	49,4	9,6	63,2	12,9	66,5	20,3	59,2	15,7
1500	58,0	19,5	49,1	16,5	39,4	8,8	38,6	8,1	52,6	11,7	55,4	17,9	48,7	13,9
1600	43,3	16,0	35,3	13,1	25,9	6,8	24,8	6,2	37,5	9,6	41,5	14,5	34,4	11,0
1700	27,2	11,4	19,6	8,4	10,5	3,9	9,5	3,6	19,8	6,6	26,1	10,4	18,7	7,3
1800	13,1	6,3	5,9	3,3	0,9	0,5	0,6	0,2	4,7	2,4	11,9	5,6	6,2	3,1
1900	2,4	1,6	0,1	0,0	0,0	0,0	0,0	0,0	0,0	0,0	1,9	1,2	0,7	0,5

TABLE A3 Average monthly and annual sunshine duration (hours) and frequencies at Potchefstroom from Schulze (1965).

	Mean daily hours	% of possible duration	No. of days with: No sunshine	1-10% of possible	11-49% of possible	50-89% of possible	90-100% of possible
January	8,7	64	0,5	1,4	6,9	15,9	6,3
February	8,2	63	0,3	1,2	7,1	13,0	6,4
March	8,1	66	1,1	2,3	4,0	15,1	8,5
April	8,7	75	0,2	1,1	3,1	12,0	13,6
May	9,0	83	0,2	0,6	1,7	9,2	19,3
June	8,8	84	0,4	0,4	1,2	9,2	18,8
July	9,0	85	0,2	0,5	1,3	11,5	17,5
August	9,9	88	0,1	0,1	0,8	7,7	22,3
September	9,6	80	0,1	0,7	1,7	12,7	14,8
October	8,9	71	0,2	1,2	4,5	16,0	9,1
November	8,8	66	0,3	1,2	6,5	15,2	6,8
December	8,6	63	0,3	1,7	7,2	16,3	5,5
Year	8,9	74	3,9	12,4	46,0	153,8	148,9

TABLE A4 Mean monthly sunshine duration for each hour (in decimals) at Potchefstroom from Schulze (1965).

hour ending	January	February	March	April	May	June	July	August	September	October	November	December	Year
0600	,22	,05								,02	,18	,25	,06
0700	,63	,55	,34	,31	,07	,00	,03	,17	,33	,57	,66	,63	,35
0800	,69	,67	,68	,78	,78	,69	,73	,91	,83	,73	,72	,72	,74
0900	,71	,70	,71	,81	,86	,88	,87	,93	,87	,75	,76	,73	,80
1000	,77	,78	,79	,83	,89	,92	,92	,96	,90	,82	,77	,79	,84
1100	,80	,77	,82	,86	,92	,94	,94	,98	,92	,83	,82	,79	,87
1200	,81	,75	,82	,85	,92	,95	,95	,98	,92	,84	,81	,79	,87
1300	,78	,75	,81	,86	,92	,94	,94	,97	,93	,83	,80	,75	,86
1400	,74	,73	,77	,84	,91	,92	,91	,96	,92	,82	,76	,69	,83
1500	,70	,68	,73	,81	,89	,90	,92	,94	,90	,77	,68	,67	,80
1600	,62	,62	,68	,78	,87	,88	,91	,93	,87	,72	,65	,56	,76
1700	,57	,55	,61	,73	,82	,78	,81	,89	,80	,67	,55	,52	,69
1800	,50	,50	,39	,30	,15	,02	,06	,24	,38	,50	,40	,49	,34
1900	,20	,13								,04	,18	,24	,07

TABLE A5 Daily and monthly mean and extreme temperature data for Lichtenburg (°C) from Weather Bureau (1954).

	mean of daily maximum	mean of highest monthly maximum	mean of daily minimum	mean of lowest monthly minimum	mean of max + min/2	mean of daily range	extreme maximum	extreme minimum	lowest maximum	highest minimum
Period*	20	20	20	20	20	20	46	46	20	20
January	28,1	33,3	15,1	10,7	21,6	13,0	37,2	6,3	17,8	21,7
February	27,4	31,6	14,9	10,9	21,2	12,5	35,0	3,9	17,2	22,2
March	26,0	30,2	13,2	7,8	19,6	12,8	34,4	1,7	15,0	18,4
April	23,7	28,2	9,3	2,2	16,5	14,4	31,7	-3,3	12,2	17,2
May	20,9	25,5	5,0	-1,4	12,9	15,9	28,9	-7,2	7,2	14,4
June	18,4	22,9	1,6	-3,8	10,0	16,8	30,0	-9,4	7,2	12,2
July	18,3	23,0	1,7	-4,4	10,0	16,6	25,6	-10,0	7,8	10,6
August	21,6	26,6	4,6	-2,4	13,1	17,0	29,4	-7,8	11,1	13,3
September	24,8	30,8	8,0	-0,4	16,4	16,8	35,0	-3,9	8,9	17,2
October	27,1	32,7	11,6	4,4	19,4	15,5	35,0	0,0	11,1	18,9
November	27,6	33,0	13,0	6,3	20,3	14,6	36,7	0,0	15,0	20,6
December	28,1	32,6	14,5	8,0	21,3	13,6	37,2	3,9	15,6	20,6
Year	24,3		9,4		16,9	14,9	37,2	-10,0	7,2	22,2

* 20-year period from 1931 to 1950
46-year period from 1905 to 1950

TABLE A6 Monthly mean, maximum and minimum grass minimum temperature (^{o}C) at Potchefstroom from Schulze (1965).

	mean	maximum	minimum
January	11,9	18,4	-1,8
February	11,8	17,8	3,8
March	8,4	16,6	0,5
April	4,9	13,1	-7,2
May	-0,7	12,0	-10,4
June	-5,3	8,9	-16,0
July	-5,2	7,8	-17,0
August	-3,3	8,9	-15,2
September	1,5	12,2	-13,5
October	6,7	15,6	-6,7
November	8,9	17,3	-4,5
December	11,0	17,0	-1,9
Year	4,2	18,4	-17,0

TABLE A7 Monthly mean soil temperature (°C) at Potchefstroom from Schulze (1965).

Time	0800 hrs					1400 hrs		2000 hrs	
Depth (cm)	10	20	30	60	120	10	20	10	20
January	22,5	23,9	24,8	25,2	23,6	29,6	25,8	28,1	27,7
February	22,2	23,7	24,6	25,1	23,8	29,1	25,5	28,7	27,7
March	21,4	22,3	23,1	24,1	23,6	27,2	24,0	26,5	25,9
April	17,0	19,0	20,0	21,6	22,2	23,4	20,5	22,5	22,5
May	11,8	14,0	15,5	17,2	19,5	17,7	15,3	17,0	17,0
June	8,3	10,3	11,6	13,8	16,7	13,7	11,4	13,3	13,2
July	8,3	10,1	11,2	12,8	14,9	13,9	11,2	13,5	13,2
August	10,5	12,3	13,4	14,3	15,0	17,1	13,7	16,7	16,1
September	14,6	16,1	16,9	17,3	16,6	21,5	17,8	21,0	20,3
October	18,9	21,3	21,2	21,5	19,3	26,3	22,5	24,8	24,1
November	21,0	22,1	23,0	23,4	21,4	29,1	24,6	26,8	26,1
December	22,0	23,2	24,1	24,4	22,6	29,9	25,6	28,0	27,2
Year	16,5	18,1	19,1	20,1	19,9	23,2	19,8	22,2	21,7

TABLE A8 Mean monthly rainfall in mm (r) and mean number of days with rain (d) at the seven stations with recording periods of over 20 years within the study area from Weather Bureau (1965).

Station name and period (in years)		Rietfontein (28)	Rooijantjiesfontein (31)	Lichtenburg TNK (57)	Lichtenburg MUN (56)	Leeuwfontein (36)	Welgevonden (34)	Putfontein (31)
January	(r)	105,3	101,2	109,4	112,3	104,5	99,7	109,5
	(d)	10	10	10	10	8	6	10
February	(r)	104,3	105,4	92,2	96,5	89,8	91,4	93,2
	(d)	9	9	9	8	7	6	8
March	(r)	91,5	80,4	92,9	94,0	93,4	86,7	83,6
	(d)	9	9	9	8	7	6	9
April	(r)	45,9	49,5	38,7	36,5	41,6	31,7	31,5
	(d)	5	5	5	4	4	2	4
May	(r)	20,8	19,7	17,7	18,0	21,2	16,8	13,4
	(d)	3	3	3	1	2	1	3
June	(r)	10,6	9,4	6,4	6,9	5,9	7,2	2,8
	(d)	1	1	1	1	1	1	1
July	(r)	5,7	4,7	6,5	6,1	6,5	3,7	6,6
	(d)	1	1	1	1	1	1	1
August	(r)	6,0	5,6	5,1	6,0	2,4	1,9	6,1
	(d)	1	1	1	1	1	1	1
September	(r)	14,7	12,3	15,0	14,8	14,3	15,5	12,7
	(d)	2	2	2	1	1	1	2
October	(r)	53,6	42,5	46,2	45,6	40,4	41,2	39,9
	(d)	6	5	5	5	5	4	4
November	(r)	69,4	68,5	73,4	69,0	66,8	71,4	64,3
	(d)	8	8	8	7	6	5	7
December	(r)	97,0	88,3	98,4	95,2	99,2	80,9	87,4
	(d)	9	9	10	9	8	5	9
Year	(r)	624,8	537,5	601,9	600,9	586,0	548,1	551,0
	(d)	64	63	64	56	51	39	59

TABLE A9 Mean monthly rainfall in mm (r) and mean number of days with rain (d) at nine weather stations with recording periods of over 20 years near the study area from Weather Bureau (1965).

Station name and period (in years)		Potchefstroom SAR (40)	Ventersdorp MAG (24)	Ottosdal POL (48)	Hartbeesfontein SKL (48)	Klerksdorp (36)	Mafeking TNK (59)	Slurry (45)	Zeerust (49)	Koster POL (50)
January	(r)	106,7	107,2	101,4	113,2	107,2	101,5	98,8	104,0	103,1
	(d)	9	12	7	9	12	9	10	13	8
February	(r)	96,3	95,8	97,7	104,5	93,7	84,4	79,7	97,0	99,4
	(d)	8	10	6	7	11	8	9	11	7
March	(r)	82,8	85,6	85,7	97,9	81,0	87,5	85,9	91,0	94,3
	(d)	8	11	6	7	10	8	9	11	7
April	(r)	37,9	34,3	38,2	38,7	37,3	40,5	36,0	37,0	40,7
	(d)	3	4	3	3	5	4	5	6	3
May	(r)	16,8	14,0	18,0	18,4	16,8	14,9	16,6	19,3	20,2
	(d)	2	3	2	2	3	2	3	3	1
June	(r)	7,9	2,5	6,6	7,8	4,6	5,6	7,5	6,4	11,0
	(d)	1	1	1	1	1	1	1	1	1
July	(r)	9,7	7,6	7,6	6,7	6,3	4,5	3,4	4,3	7,5
	(d)	1	1	1	1	1	1	1	1	1
August	(r)	9,9	8,4	7,8	6,7	8,6	4,6	3,0	7,1	8,5
	(d)	1	1	1	1	1	1	1	1	1
September	(r)	19,8	17,5	12,3	16,0	16,5	17,0	15,3	15,4	18,4
	(d)	2	2	1	2	3	2	2	2	2
October	(r)	49,5	51,6	40,0	40,6	42,7	41,2	42,5	42,6	47,6
	(d)	6	7	4	4	6	5	5	7	6
November	(r)	77,2	69,3	64,6	67,3	73,9	64,5	64,5	76,7	88,2
	(d)	8	9	5	7	9	7	7	9	7
December	(r)	97,5	94,5	89,7	94,7	94,0	99,9	97,0	96,5	115,2
	(d)	8	11	7	7	11	8	9	10	8
Year	(r)	612,0	588,2	569,6	612,5	582,6	566,1	550,2	597,3	654,1
	(d)	57	72	44	51	74	56	62	75	52

TABLE A10 Mean monthly rainfall (mm) for districts 19 and 21 from Weather Bureau (1960a) and for district 84 from van Rooy (1972).

	district			
	19	21	84	84 (5)
January	84,0	108,0	99,8	16,2%
February	85,9	97,3	90,5	16,4%
March	81,5	87,4	90,4	13,9%
April	36,3	35,3	45,6	8,2%
May	15,8	18,1	20,2	3,2%
June	5,6	7,1	8,5	1,6%
July	5,4	7,2	6,0	1,1%
August	6,4	7,4	4,5	0,6%
September	12,0	15,6	14,2	2,3%
October	33,6	48,8	42,3	7,2%
November	53,0	81,6	75,9	13,2%
December	69,5	98,4	93,3	16,1%
Annual mean	488,8 (1)	611,8 (1)	591,3 (1)	
Annual mean			588,5 (2)	
			148% (3)(1)	
			164% (3)(2)	
			68% (4)(1)	
			60% (4)(2)	

(1) Year ending 31st December

(2) Year ending 30th June

(3) Maximum annual district rainfall as % of mean

(4) Minimum annual district rainfall as % of mean

(5) Mean district rainfall for 12 equal months as % of

TABLE A11 Frequency of droughts of different duration for twelve monthly precipitations below 75% of the average annual rainfall from Weather Bureau (1960a).

District	Drought duration in months											%
	1	2	3	4	5	6	7	8	9	10	11	
19	6	1	3	1	.	.	1	1	1	1	1	13,4
21	3	5	.	.	.	.	1	1	1	.	1	9,5

% = Total number of drought months as a percentage of the total number of months covered by the data

TABLE A12 Variability (V) and reliability (R) of rainfall within districts 19 and 21 and maxima (MAX) and minima (MIN) over all districts (period 1907 - 1946) from Weather Bureau (1960a).

	Variability (V)			Reliability (R)		
	January	June	Year	January	June	Year
District 19	0,405	1,253	0,188	0,636	0,140	0,820
District 21	0,337	1,329	0,188	0,691	0,113	0,821
MAX	0,933	1,329	0,342	0,797	0,647	0,890
MIN	0,214	0,391	0,113	0,285	0,113	0,723

TABLE A13 Mean monthly vapour pressure (V) and mean monthly saturation deficit (S) in mb at Potchefstroom from Weather Bureau (1954).

Time	0800		1400	
	V	S	V	S
January	16,2	7,9	14,4	23,4
February	16,7	5,8	16,4	17,8
March	16,1	4,0	14,5	17,0
April	12,1	4,0	11,0	18,7
May	8,5	3,0	8,5	15,9
June	6,1	2,4	6,8	13,8
July	5,8	2,7	6,2	14,6
August	6,9	4,7	7,3	17,7
September	8,0	8,1	8,0	22,9
October	11,9	9,4	9,2	26,2
November	13,5	9,7	10,9	23,3
December	15,3	9,4	12,8	22,8
Year	11,4	5,9		

TABLE A14 **Mean monthly and annual values of relative humidity (%)** for six times of day at Mafeking from Weather Bureau (1954).

	time (hours)					
	0600	0900	1200	1500	1800	2100
January	81	60	48	43	46	67
February	86	69	56	49	55	74
March	90	67	53	45	54	79
April	85	57	40	35	49	71
May	81	58	38	33	46	65
June	77	54	36	30	45	62
July	71	49	30	26	36	55
August	62	42	26	21	26	43
September	56	38	27	22	26	40
October	63	45	34	30	34	49
November	72	48	38	32	37	55
December	67	43	30	26	29	43
Year	74	53	38	33	40	59

GROUP CONSTITUTIONS

Total association analysis (after re-allocation)

Group	No. of quadrats	Quadrat numbers									
1	10	18	20	25	32	34	37	81	82	87	93
2a	19	6	44	45	46	48	49	51	53	55	56
		57	58	59	61	62	64	73	86	98	
2b	18	1	5	7	10	36	41	47	50	52	60
		65	67	71	78	88	96	97	99		
3a	10	17	28	35	39	42	68	76	79	83	95
3b	24	3	8	12	13	15	19	21	22	23	24
		26	27	29	30	31	54	63	70	72	74
		91	92	94	107						
4a	9	2	11	14	16	40	69	77	84	90	
4b	21	111	114	116	121	122	123	125	127	128	131
		133	134	135	136	137	138	139	140	161	194
		211									
5a	3	38	80	167							
5b	26	4	33	43	109	110	112	132	153	155	162
		166	168	171	189	192	193	196	201	203	204
		207	208	215	216	217	218				
6a	6	89	118	119	124	130	210				
6b	7	66	85	102	104	105	106	113			
7a	15	120	141	142	143	144	145	147	148	149	151
		152	154	158	159	160					
7b	3	115	219	220							
7c	9	9	75	103	108	117	129	191	202	212	
8	11	100	101	146	164	165	169	170	199	209	213
		214									
9a	12	126	150	156	157	163	173	174	175	176	184
		186	190								
9b	10	182	185	187	188	195	197	198	200	205	206
9c	7	172	177	178	179	180	181	183			

Bankenveld association analysis

Group	No. of quadrats	Quadrat numbers									
1	12	1	5	6	7	18	20	21	22	31	54
		65	70								
2a	3	71	96	98							
2b	14	44	45	47	48	49	50	53	56	57	59
		60	62	67	86						
2c	6	38	46	51	55	64	68				
2d	10	10	24	58	61	73	76	82	88	93	110
3	11	30	32	41	43	52	78	79	80	81	97
		99									
4	17	13	15	25	26	27	29	34	36	37	39
		63	72	74	75	77	92	94			
5	9	8	17	19	28	40	42	69	83	95	
6	12	14	16	66	84	85	87	89	91	100	101
		102	104								
7	16	2	3	4	9	11	12	23	33	35	90
		103	105	106	107	108	109				

AXOR classification at 10-group level

Group	No. of quadrats	Quadrat numbers									
A	12	38	41	44	45	46	48	50	51	56	64
		67	73								
B	12	6	49	53	55	57	58	59	60	62	86
		88	98								
C	8	52	61	80	81	82	93	99	110		
D	10	10	24	31	36	47	68	71	78	96	97
E	5	1	5	7	34	70					
F	12	2	3	9	11	14	16	23	33	66	100
		107	108								
G	12	84	85	87	89	90	91	101	102	103	104
		105	106								
H	14	4	32	35	37	39	40	43	69	74	75
		77	79	92	109						
I	7	17	28	42	76	83	94	95			
J	18	8	12	13	15	18	19	20	21	22	25
		26	27	29	30	54	63	65	72		

DIVINF classification at 8-group level

Group	No. of quadrats	Quadrat numbers									
A	17	6	44	45	46	48	49	51	53	55	56
		57	59	62	64	68	86	98			
B	18	1	5	7	31	34	38	41	47	50	60
		67	70	71	78	81	96	97	99		
C	16	10	18	20	21	22	24	54	58	61	65
		73	76	82	88	93	110				
D	10	9	14	84	85	101	102	103	105	106	108
E	20	2	3	4	8	11	12	13	15	16	19
		23	27	29	33	63	66	69	72	100	107
F	9	25	26	28	37	74	80	83	92	94	
G	13	17	30	32	35	36	39	40	43	52	75
		77	79	109							
H	7	42	87	89	90	91	95	104			

LIST OF PLANTS COLLECTED AND RECORDED IN QUADRATS

The following plants were either recorded as present in quadrats during sampling or were collected by J.W. Morris (M and ML prefixes to collector numbers), Morris and C. Boucher (M&B), Morris and G.J. Engelbrecht (M&E) and Morris and D. Müller (M&M) during the course of fieldwork in the South-western Transvaal. Species recorded from quadrats but not collected within the study area are marked with an asterisk. The list is not comprehensive but most permanently-recognisable grasses and herbs as well as most woody plants are considered to have been collected during the three-year period of fieldwork.

Specimens are lodged with the National Herbarium, Botanical Research Institute, Pretoria (PRE) and duplicates of most collections are housed in the office of the Extension Officer, Department of Agricultural Technical Services, Lichtenburg, Transvaal.

Families and genera of Spermatophyta are arranged according to Phillips (1951), based on de Dalla Torre & Harmse (1900-1907). The 309 infrageneric categories are arranged alphabetically within families.

P T E R I D O P H Y T A

FILICALES

ADIANTACEAE

	collectors numbers
Pelaea calomelanos (Swartz) Link	M&E 1166

S P E R M A T O P H Y T A

ANGIOSPERMAE

POACEAE

Trachypogon spicatus (L.f.) Kunze	M&E 1084
Elionurus argenteus Nees	M&E 1097
Andropogon appendiculatus Nees	M&E 1042
Andropogon schirensis Hochst. ex A. Rich.	M&E 1172
Andropogon schirensis var. angustifolius Hochst.	M&E 1045
* Diheteropogon amplectens (Nees) Clayton	M 1128
Schizachyrium sanguineum (Retz.) Alst.	M&E 1171
* Cymbopogon excavatus (Hochst.) Stapf ex Burtt Davy	M 1104
Cymbopogon plurinodis (Stapf) Stapf ex Burtt Davy	M&E 1000
Hyparrhenia filipendula (Hochst.) Stapf var. pilosa (Hochst.) Stapf	M&E 1078
Hyparrhenia hirta (L.) Stapf	M&E 1173
Hyparrhenia sp.	ML 28
Heteropogon contortus (L.) Beauv. ex Roem.& Schult.	M&E 1044
Themeda triandra Forsk.	M&E 1029, M&E 1136
Anthephora pubescens Nees	M&E 1022
Tragus racemosus (L.) All.	M&E 1048
Paspalum dilatatum Poir.	M&E 1179

ж	Panicum coloratum L.	M 1066
	Panicum maximum Jacq.	M&E 1314
	Panicum stapfianum Fource.	M&E 1063
	Urochloa panicoides Beauv.	M&E 1190
	Brachiaria marlothii (Hack.) Stent	M&E 1089
	Brachiaria serrata (Spreng.) Stapf	M&E 1040
	Digitaria argyrograpta (Nees) Stapf	M&E 1075
	Digitaria tricholaenoides Stapf	M&E 1295
	Rhynchelytrum repens (Willd.) C.E. Hubb.	M&E 1163
	Rhynchelytrum setifolium (Stapf) Chiov.	M&E 1307
	Rhynchelytrum villosum (Parl.) Chiov.	M&E 1071, M 1145
	Setaria flabellata Stapf	M&E 1023
	Setaria nigrirostris (Nees) Dur. & Schinz	M&E 1123
	Setaria pallide-fusca (Schumach.) Stapf & C.E. Hubb.	M&E 1169
	Setaria sp.	M 1146
	Leersia hexandra Swartz	M&E 1192
	Aristida canescens subsp. canescens Henr.	M&E 1006
	Aristida congesta Roem. & Schult. subsp. congesta	M&E 1064, M&E 1096
	Aristida diffusa Trin. var. burkei (Stapf) Schweick.	M&E 1019, M&E 1088
	Stipagrostis uniplumis (Licht.) De Wint. var. neesii (Trin. & Rupr.) De Wint.	M&E 1043
	Sporobolus africanus (Poir.) Robyns & Tournay	M&E 1018
	Sporobolus ludwigii Hochst.	M&M 22
ж	Sporobolus pectinatus Hack.	
	Loudetia simplex (Nees) C.E. Hubb.	M&E 1281

	Microchloa caffra Nees	M&E 1076
	Cynodon dactylon (L.) Pers.	M&E 1137
	Chloris radiata (L.) Swartz	M&E 1074
	Eustachys mutica (L.) Cufod.	M&E 1010, M&E 1062
	Enneapogon desvauxii Beauv.	M&E 1334
	Triraphis andropogonoides (Steud.) Phill.	M&E 1077
	Triraphis schlechteri Pilg. ex Stent	M&E 1004
	Fingerhuthia africana Lehm.	M&E 1033
*	Diplachne biflora Hack.	
*	Diplachne fusca (L.) Beauv. ex Stapf	M 1115
	Pogonarthria squarrosa (Licht.) Pilg.	M&E 1073
	Trichoneura grandiglumis (Nees) Ekman	M&E 1066
	Eragrostis barbinodis Hack.	M&E 1058
	Eragrostis capensis (Thunb.) Trin.	ML 27
*	Eragrostis curvula (Schrad.) Nees	M 1292
	Eragrostis gummiflua Nees	M&E 1001
*	Eragrostis lehmanniana Nees	M 1220
	Eragrostis micrantha Hack.	M&E 1194
	Eragrostis obtusa Munro ex Fical. & Hiern	M&E 1080
*	Eragrostis racemosa (Thunb.) Steud.	M 1308
	Eragrostis stapfii De Wint.	M&E 1002
	Eragrostis superba Peyr.	M&E 1060
	Eragrostis tricophora Coss & Dur.	M&E 1049
	Eragrostis sp.	M&E 1138
	Oropetium capense Stapf	M&E 1093

CYPERACEAE

Cyperus margaritaceus Vahl	M&E 1025
Cyperus marginatus Thunb.	M&E 1104, ML 16
Cyperus teneriffae Poir.	M&E 1167
Cyperus usitatus Burch.	M&E 1293
* Mariscus capensis Schrad.	M 1061
Mariscus congestus C.B. Cl.	M&E 1067, M&E 1184
Kyllinga alba Nees	M&E 1082
Fuirena pubescens Kunth	M&E 1068
Fimbristylis ovata (Burm. f.) Kern	M&E 1031
Bulbostylis burchellii (Fical. & Hiern) C.B. Cl.	M&E 1081

COMMELINACEAE

Commelina africana L.	M&E 1198
Commelina erecta L.	M&E 1197

LILIACEAE

Bulbine abyssinica A. Rich.	M&E 1092
Bulbine caespitosa Bak.	M&E 1193
* Bulbine sp.	
Anthericum cooperi Bak.	M&E 1005
Trachyandra laxa (N.E. Br.) Oberm. var. erratica (Oberm.) Oberm.	M&E 1209
Dipcadi marlothii Engl.	M&E 1210
Dipcadi viride (L.) Moench	M&E 1125
Asparagus laricinus Burch.	M&E 1119, M&E 1124

HYPOXIDACEAE

* Hypoxis sp.

IRIDACEAE

Tritonia nelsonii Bak. M&E 1199

Gladiolus permeabilis Delaroche var. edulus (Burch. ex Ker) Oberm. M&E 1103

ORCHIDACEAE

Habenaria epipactidea Reichb. f. M&E 1102

ULMACEAE

Celtis africana Burm. f. M&E 1127

LORANTHACEAE

Viscum verrucosum Harv. M&E 1201

SANTALACEAE

Thesium asterias A.W. Hill M&E 1287

Thesium costatum A.W. Hill M&E 1038

POLYGONACEAE

Oxygonum alatum Burch. M&E 1206

Oxygonum dregeanum Meisn. var. dregeanum M&E 1070

CHENOPODIACEAE

Atriplex semibaccata R. Br. ML 20

Lophiocarpus polystachyus Turcz. M&M 19

AMARANTHACEAE

Sericorema remotiflora (Hook. f.) Lopr. M&E 1282

Cyphocarpa angustifolia Lopr. M&E 1072

Aerva leucura Moq. M&M 21, M&M 28, M&M 32, M&E 1091

* Brayulinea densa (Homb. & Bonpl.) Small M&B 232a

AIZOACEAE

Limeum fenestratum (Fenzl) Heim. M&E 1325

MESEMBRYANTHACEAE

Ruschia hamata (L. Bol.) Schwant.	ML 19
Ruschia rigens L. Bol.	ML 22
Aloinopsis sp.	ML 15

PORTULACEAE

* Talinum arnotii Hook. f.	M&E 1161
Anacampseros telephiastrum DC.	M&E 1270
Portulaca kermesina N.E. Br.	M&E 1196
Portulaca quadrifida L.	ML 24

CARYOPHYLLACEAE

Pollichia campestris Soland. in Ait.	M&E 1083

RANUNCULACEAE

Clematis brachiata Thunb.	M&E 1203
Clematopsis scabiosifolia (DC.) Hutch.	M&E 1087
Ranunculus multifidus Forsk.	M&E 1180

MENISPERMACEAE

Antizoma angustifolia (Burch.) Miers ex Harv.	M&E 1128

CRUCIFERAE

Sisymbrium thellungii Schulz	M&M 26
Erucastrum strigosum (Thunb.) Schulz	M&E 1311

CRASSULACEAE

* Crassula transvaalensis (Kuntze) K. Schum.	M&B 54

SAXIFRAGACEAE

Vahlia capensis Thunb.	M&M 12, M&E 1008, M&E 1333

ROSACEAE

Parinari capensis Harv.	M&E 1305

LEGUMINOSAE

	Acacia caffra (Thunb.) Willd.	M&E 1114
	Acacia giraffae Willd.	M 1162
	Acacia hebeclada DC. subsp. hebeclada	M 1167
	Acacia hereroensis Engl.	M&E 1130
	Acacia karroo Hayne	M&E 1113, M 1151
*	Acacia robusta Burch.	M 1084
	Cassia mimosoides L.	M&E 1007
	Pearsonia cajanifolia (Harv.) Polhill (in MS.)	M&E 1205
	Pearsonia uniflora Kensit (in MS.)	M&E 1272, M&E 1276
	Melolobium microphyllum Eckl. & Zeyh.	M&M 20
*	Elephantorrhiza elephantina (Burch.) Skeels	M 1252
	Medicago aschersoniana Urb.	M&E 1188
	Trifolium africanum Ser.	M&E 1186
	Indigofera daleoides Benth.	M&E 1297
	Indigofera disticha Eckl. & Zeyh.	M&M 25
	Indigofera filipes Benth.	M&E 1271
	Indigofera heterotricha DC.	M&E 1017
	Indigofera macra E. Mey.	M&E 1020
	Tephrosia capensis (Jacq.) Pers.	M&M 30
*	Tephrosia longipes Meisn.	
	Tephrosia semiglabra Sond.	M&E 1319
	Ophrestia oblongifolia (E. Mey.) H.M. Forbes	M&E 1208
*	Zornea milneana Mohl.	M 1211
	Rhynchosia confusa Burtt Davy	M&E 1279
	Rhynchosia monophylla Schltr.	M&E 1294
	Rhynchosia nervosa Benth.	M&E 1313

Rhynchosia totta (Thunb.) DC.	M&M 29, M&E 1011, M&E 1321
Eriosema burkei Benth.	M&E 1290
Vigna angustifoliolata Verdc.	M&E 1204, M&E 1298, M&E 1318

GERANIACEAE

Monsonia angustifolia E. Mey.	ML 5
Monsonia biflora DC.	M&E 1312
Pelargonium dolomiticum Knuth	M&E 1164

OXALIDACEAE

Oxalis corniculata L.	M&E 1147
Oxalis obliquifolia Steud. ex Rich.	M&E 1195

POLYGALACEAE

Polygala amatymbica Eckl. & Zeyh.	M&M 2
Polygala hottentotta Presl	M&E 1016
* *Polygala rehmannii* Chod.	M. 1309
Polygala sp. cf. *amatymbica* Eckl. & Zeyh.	M&M 23

EUPHORBIACEAE

Phyllanthus maderaspatensis L.	M&M 24
Acalypha angustata Sond. var. *glabra* Sond.	M&M 3
Acalypha sp.	M&E 1267
Jatropha zeyheri Sond.	M&E 1274
Euphorbia inequilatera Sond.	M&E 1054
Euphorbia pseudotuberosa Pax	M&E 1302
Euphorbia striata Thunb.	M&M 5
* *Euphorbia* sp.	M&B 70

ANACARDIACEAE

Ozoroa paniculosa (Sond.) R. & A. Fernandes	M&E 1086

*	Rhus lancea L. f.	M&B 291
	Rhus pyroides Burch.	M&E 1090, M&E 1202, ML 18
	CELASTRACEAE	
	Maytenus heterophylla (Eckl. & Zeyh.) N. Robson	M&E 1120
	RHAMNACEAE	
	Ziziphus mucronata Willd.	M&E 1115
	Ziziphus zeyherana Sond.	M&E 1041
	TILIACEAE	
	Corchorus asplenifolius Burch.	M&E 1100
	Grewia flava DC.	M&E 1117
	Triumfetta sonderi Fical. & Hiern	M&E 1200
	MALVACEAE	
	Sida chrysantha Ulbr.	M&E 1165
	Pavonia burchellii (DC.) R.A. Dyer	M&E 1108
*	Hibiscus microcarpus Garcke	M&E 59
	Hibiscus pusillus Thunb.	M&E 1328
	Hibiscus trionum L.	M&E 1175
	STERCULIACEAE	
*	Hermannia betonicifolia Eckl. & Zeyh.	
	Hermannia depressa N.E. Br.	M&E 1009
	Hermannia linnaeoides (Burch.) K. Schum.	M&E 1046
	Hermannia quartiniana A. Rich.	M&E 44, M&E 1098, M&E 1099
	Hermannia tomentosa (Turcz.) Schinz ex Engl.	M&E 1101
	ELATINACEAE	
	Bergia decumbens Planch. ex Harv.	M&M 15, M&E 1030

THYMELAEACEAE

* Lasiosiphon capitatus Burtt Davy

ONAGRACEAE

Oenothera rosea Ait.	M&E 1122
Oenothera tetraptera Cav.	ML 8

UMBELLIFERAE

Pituranthos burchelli (DC.) Schinz	ML 10, M&E 1139

EBENACEAE

Diospyros austro-africana De Wint. var. microphylla (Burch.) De Wint.	M&E 1028
Diospyros lycioides Desf. subsp. lycioides	M&E 1105, M&E 1116

OLEACEAE

Menodora africana Hook.	M&E 1056
Menodora sp. cf. africana Hook.	M&M 1

GENTIANACEAE

Chironia palustris Burch. subsp. palustris	M&E 1178

PERIPLOCACEAE

* Raphionacme burkei N.E. Br.

Raphionacme hirsuta (E. Mey.) R.A. Dyer ex Phill.	M&E 1027

ASCLEPIADACEAE

Schizoglossum glabrescens Schltr.	M&E 1317
Periglossum kassnerianum Schltr.	M&E 1189
Pachycarpus schinzianus N.E. Br.	M&E 1051
Asclepias eminens Schltr.	M&E 1032
Asclepias fruticosa L.	M&E 1126
cf. Asclepias sp.	M&M 4, ML 7

	Cynanchum virens A. Dietr.	M&E 1121
	Caralluma lutea N.E. Br.	M&E 1332
	CONVOLVULACEAE	
	Convolvulus ocellatus Hook. f. var. ornatus (Engl.) A. Meeuse	M&E 1052, M&E 1278
	Convolvulus thunbergii Roem. & Schult.	M&E 1296
	Merremia verecunda Rendle	M&E 1288
	Ipomoea bathycolpos Hall. f.	M&M 9, M&E 1034
*	Ipomoea obscura Ker var. fragilis A. Meeuse	
	Ipomoea ommaneyi Rendle	M&E 1292, M&E 1303
	Turbina oblongata (E. Mey. ex Choisy) A. Meeuse	M&E 1036
	BORAGINACEAE	
	Trichodesma angustifolium Harv.	ML 11, M&E 1135
	Cynoglossum enerve Turcz.	M&M 16
	VERBENACEAE	
	Verbena bonariensis L.	M&E 1174
	Lantana rugosa Thunb.	M&E 1107
	Lippia scaberrima Sond.	M&E 1026
*	Chascanum hederaceum (Sond.) Moldenke	M&B 232
	Chascanum pinnatifidum (L. f.) E. Mey.	M&E 1095
	Clerodendrum triphyllum (Harv.) Pears.	M&E 1280
	LABIATAE	
	Teucrium capense Thunb.	M&E 1132
	Acrotome inflata Benth.	M&E 1289
	Lasiocorys capensis Benth.	M&M 14, M&M 27, ML 23, ML 29
	Stachys spathulata Burch. ex Benth.	M&E 1065

	Salvia radula Benth.	M&E 1059
	Coleus neochilus (Schltr.) Codd	M&E 1094, M&E 1269

SOLANACEAE

	Solanum incanum L.	M&E 1112
	Solanum panduraeforme E. Mey.	M&E 1111
*	Solanum supinum Dun.	M&B 171

SCROPHULARIACEAE

	Aptosimum depressum Burch. var. elongatum Hiern	ML 25, ML 26
	Aptosimum indivisum Burch.	ML 1
	Sutera atropurpurea (Benth.) Hiern	M&E 1055
	Sutera aurantiaca (Burch.) Hiern	M&E 1057
	Zaluzianskya maritima Walp.	M&E 1268
*	Selago holubii Rolfe	M 1227
	Walafrida paniculata Rolfe	M&E 1014
	Walafrida saxatilis (E. Mey.) Rolfe	M&E 1182
	Striga elegans Benth.	M&E 1168
	Striga gesnericides (Willd.) Vatke	M&E 1284

PEDALIACEAE

	Pterodiscus speciosus Hook.	M&E 1003
	Sesamum capense Burm. f.	M&E 1106

ACANTHACEAE

*	Chaetacanthus costatus Nees	
	Crabbea angustifolia Nees	M&E 1013, M&E 1263
	Crabbea hirsuta Harv.	ML 2
*	Barleria macrostegia Nees	M 1152
	Barleria pretoriensis C.B. Cl.	M&E 1320
	Blepharis angusta (Nees) T. Anders.	M&E 1021
	Blepharis innocua C.B. Cl.	M&M 10, M&E 1291

* *Blepharis integrifolia* (L. f.) E. Mey. M 1253

Blepharis squarrosa (Nees) T. Anders. M&E 1035

Blepharis transvaalensis Schinz M&E 1299

Justicia anagaloides T. Anders. M&E 1015, M&E 1213

PLANTAGINACEAE

Plantago lanceolata L. M&E 1187

RUBIACEAE

Kohautia lasiocarpa Klotzsch M&E 1037

* *Kohautia omahekensis* (Krause) Brem M&B 258

Kohautia sp. M&E 1336

Xeromphis rudis (E. Mey. ex Harv.) Codd M&E 1118

* *Pentanisia* sp.

Pygmaeothamnus zeyheri (Sond.) Robyns M&E 1079, M&E 1304

* *Anthospermum rigidum* Eckl. & Zeyh. M 1249

DIPSACACEAE

Scabiosa columbaria L. M&M 8, M&E 1024

CUCURBITACEAE

Cucumis heptadactylus Naud. M&E 1310

Cucumis hirsutus Sond. M&E 1301

Cucumis myriocarpus Naud. M&E 1316

Cucumis zeyheri Sond. M&E 1085

CAMPANULACEAE

Wahlenbergia caledonica Sond. M&E 1324

Wahlenbergia lycopodioides Schltr. & von Brehm. M&M 6, ML 3

Lightfootia denticulata (Burch.) Sond. M&E 1207

LOBELIACEAE

	Cyphia assimilis Sond.	M&E 1331
	Lobelia thermalis Thunb.	M&E 1183, M&M 17

COMPOSITAE

*	Vernonia oligocephala (DC.) Sch. Bip. ex Walp.	M&B 229
	Felicia muricata (Thunb.) Nees	M&E 1131, M&E 1273
	Nidorella hottentotica DC.	M&E 1047, M&E 1264, M&E 1306
	Conyza podocephala DC.	M&E 1012
*	Nolletia ciliaris (DC.) Steetz	M&B 27
	Chrysocoma tenuifolia Berg.	M&E 1129
	Tarchonanthus camphoratus L.	M&E 1315
	Gnaphalium undulatum L.	M&E 1283
*	Helichrysum caespititium Sond.	M 1192
*	Helichrysum cerastioides DC.	M&B 155
	Helichrysum dregeanum Sond. & Harv.	M&E 1244, ML 17
	Helichrysum nudifolium (L.) Less.	M&M 11
	Helichrysum rugulosum Less.	M&E 1327
*	Helichrysum zeyheri Less.	M 1204
	Geigeria aspera Harv.	M&E 1053
	Geigeria brevifolia (DC.) Harv.	M&E 1069
*	Geigeria burkei Harv.	M 1114
	Zinnia peruviana (L.) L.	M&E 1109
	Schkuhria pinnata (Lam.) Kuntze	M&E 1308
	Pentzia globosa Less.	M&E 1330
	Hertia ciliata (Harv.) Kuntze	M&M 31
	Senecio burchellii DC.	M&E 1335

*	Senecio coronatus (Thunb.) Harv.	
	Senecio hydrorrhizus C.A. Smith	M&E 1177
	Senecio orbicularis Sond.	M&E 1277
*	Senecio venosus Harv.	
	Castalis spectabilis (Schltr.) T. Norl.	M&E 1300
	Osteospermum muricatum E. Mey.	ML 6
	Osteospermum scariosum DC.	ML 9
	Ursinia nana DC. subsp. leptophylla Prassler	M&E 1162
	Arctotis venusta T. Norl.	M&E 1050
	Haplocarpha scaposa Harv.	ML 14
*	Gazania krebsiana Less.	M&E 35
	Berkheya onopordifolia (DC.) O. Hoffm. ex Burtt Davy	M&E 1181, M&E 1326
	Berkheya pinnatifida (Thunb.) Thell. subsp. stobaeoides (Harv.) Roessl.	M&E 1061, M&E 1176
	Cirsium vulgare (Savi) Ten.	M&E 1185
	Dicoma anomala Sond.	M&E 1039
*	Dicoma macrocephala DC.	M&B 29