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The Ecological Profiles Technique applied to data from Lichtenburg, South Africa

J. W. MORRIS* AND J.-L. GUILLERM†

ABSTRACT

The method of ecological profiles and information shared between species and ecological variables, developed in France, is described for the first time in English. Preliminary results, using the technique on Bankenveld quadrat data from Lichtenburg, Western Transvaal, are given. It is concluded that the method has great potential value for the understanding of the autecology of South African species provided that the sampling method is appropriate.

INTRODUCTION

Presently, one of the most commonly used ecological synthesis techniques at the Centre d'Etudes Phytosociologiques et Ecologiques (C.E.P.E.), Montpellier, is that of ecological profiles and information shared between species and ecological variables (Profils écologiques et information mutuelle entre espèces et facteurs écologiques). As the writers consider that the technique deserves trial by other than French-speaking ecologists, it is described below in detail. This account is the first known in English. South African data are used to illustrate its utility.

The first account of the method was given by Godron (1965) and since then more detailed accounts have been prepared by Godron (1968), Daget *et al.* (1972), Guillerm (1969 a, b and c) and by Guillerm (1971), all of which have been in French. Both floristic and habitat data from samples are used in this univariate technique. According to Daget *et al.* (1972), and others, its main application is sampling improvement, but this is by no means its only use.

SAMPLE AREA AND DATA USED

The 110 × 4 m quadrats (in this account 'quadrat' is used for 'sample', 'relevé', etc.) used in the study, were laid out in a stratified random manner near Lichtenburg, Western Transvaal, within the 2626AA quarter-degree square. Details of the area and field sampling method are given in Morris (1973). The vegetation is classed as Bankenveld by Acocks (1953).

Floristic data consisted of presence within the quadrats of 229 species. The 12 ecological variables listed in Table 1 were coded for analysis. The first eight are acceptable habitat variables. Soil colour (the ninth variable) was included as a control; it was not expected that it would be ecologically meaningful in its own right. Total basal cover was that of all grass and herb strata combined and the strata of variables 11 and 12 are those defined by Godron *et al.* (1968). For the purpose of this paper, basal cover was considered an environmental variable although it is usually considered as a structural property of the vegetation. Cover was used in this way as so few ecological variables were available. As the variables were not originally recorded for analysis by this technique, there was not always enough information available to code according to the specifications of Godron *et al.* (1968). Topographic position, apparent biotic influence, soil pH and soil HC1 reaction were coded according to Godron *et al.* Aspect, soil depth and soil colour were coded in the same way, although the total number of classes was later reduced in the analysis. As there is little topography in the Lichtenburg area, the following special scale was used for slope: 0=no slope, 1= slight (less than 1%), 2=1% or more. Amount of surface rock was coded as: 1=none, 2=few, 3=moderate, 4=many rocks. Total basal cover was recorded on the following scale: 2=5–9,9%, 3=10–14,9%, 4=15–19,9%, 5=20–24,9%. Basal cover for individual strata was recorded as: 0=0%, 1=1–2%, 2=3–4% 3=5–6%.........etc. Two strata, corresponding with strata II and IV of Godron *et al.*, were recognized.

TABLE 1. Ecological variables used in the analysis and the number of classes of each.

Code No.	Variable	Initial 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 rocks.................	4	4
6.	Soil depth....................	11	6
7.	Soil pH.......................	4	4
8.	Soil HC1 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

ECOLOGICAL VARIABLES AND EQUITABILITY OF SAMPLING

The first step is the calculation of the comprehensive profile (CP) for each ecological variable. The CP is a list of all the classes of a variable and the frequency of occurrence of quadrats in each class. An example of a CP is given in Table 2 where there are a total of N quadrats.

TABLE 2. Comprehensive profile for a variable with K classes.

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

Comprehensive profiles for the 12 variables of this study are given in Table 3. The CP gives the distribution of absolute frequency. Relative frequency is obtained by dividing each frequency by N. If the absolute frequency is not too low, a good estimate of probability of occurrence may be obtained from the relative frequencies. If the environmental gradient has been well sampled, quadrats will be equally distributed through the classes of the CP and, hence, the probabilities of occurrence will be approximately equal. A variable for which quadrats have equal probabilities

* Botanical Research Institute, Department of Agricultural Technical Services, Private Bag X101, Pretoria.

† Centre d'Etudes Phytosociologiques et Ecologiques L. Emberger, B.P. 5051, Montpellier 34, France.

TABLE 3. Comprehensive profiles for variables used in the analysis. Class numbers (from Godron *et al.*, 1968) do not apply to variables marked with an asterisk.

Variable	Class number										
	0	1	2	3	4	5	6	7	8	9	10
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. HC1 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		

of being in each class is said to have a high indetermination (M. Godron, pers. comm., 1973). Indetermination may be estimated by calculating the entropy (I_L) (see Abramson, 1963) 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 2. The formula can also be expressed in the form:

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

(FORTRAN IV programmes written at C.E.P.E. for the ecological profiles technique have been modified for local computers. Listings and card decks are available from the senior author).

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

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

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

From the entropy of a variable (I_L) and maximum entropy ($I_{max,L}$) it is possible to judge equitability of sampling. Equitability is the degree to which quadrats cover the variation of a factor with the given class intervals. The fraction (Q_L) is used:

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

Usually, the higher the value of Q, the better the sampling of the total variation within the sample area. The fraction should, however, be used with caution as some variables have misleading Q values. The problem arises when one is dealing with variables with many classes: for example, the 125 soil types in 'Code pour le relevé methodiqué' of Godron *et al.* Many classes will be unsampled, or very poorly represented in the CP. The value of I_{max} should be based on the number of classes sampled adequately.

After studying the CP's for the 12 variables used here, the number of classes was reduced for five of them (see Table 1) as certain class frequencies were very low. In the cases 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, were retained. The other 6/ codes and the 7/, 5/, and 4/ codes were grouped into four classes on the basis of the 'simplified' wavelength code of Godron *et al.* It has been suggested by M. Godron (pers. comm., 1973) that inspection of corrected frequency profiles (see later) may assist in deciding which classes should be grouped. The observed and maximum entropy for each variable and values for Q are given in Table 4.

TABLE 4. 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 HC1 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

Variables which are equitably sampled according to the Q criterion, include, in order of decreasing importance, biotic influence, surface rock, basal cover for strata IV and II, and soil pH.

Observed entropy has been plotted against maximum entropy for each variable in Fig. 1. The nearer a variable 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.

To improve equitability of sampling, Daget *et al.* (1972) suggest resuming stratification of the vegetation where it was stopped, starting with the variables known to be poorly sampled. In the choice of variables, one is also guided by the calculation of mutual information between species and variables, which permits the detection of variables of ecological importance.

MUTUAL INFORMATION BETWEEN SPECIES AND ECOLOGICAL VARIABLES

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 (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 variable by the CP. Absolute frequency may yield misleading results as it is directly proportional to the total number of occurrences, therefore it is better to use relative frequency 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 given by U_1/R_1.

Further to 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 found by multiplying relative frequency by the inverse of average relative frequency over all quadrats:

$$C_i = \frac{U_i}{R_i} \cdot \frac{N}{U_T}$$

(see Table 5 for explanation of symbols)

TABLE 5. 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	$U_T + V_T = N$

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

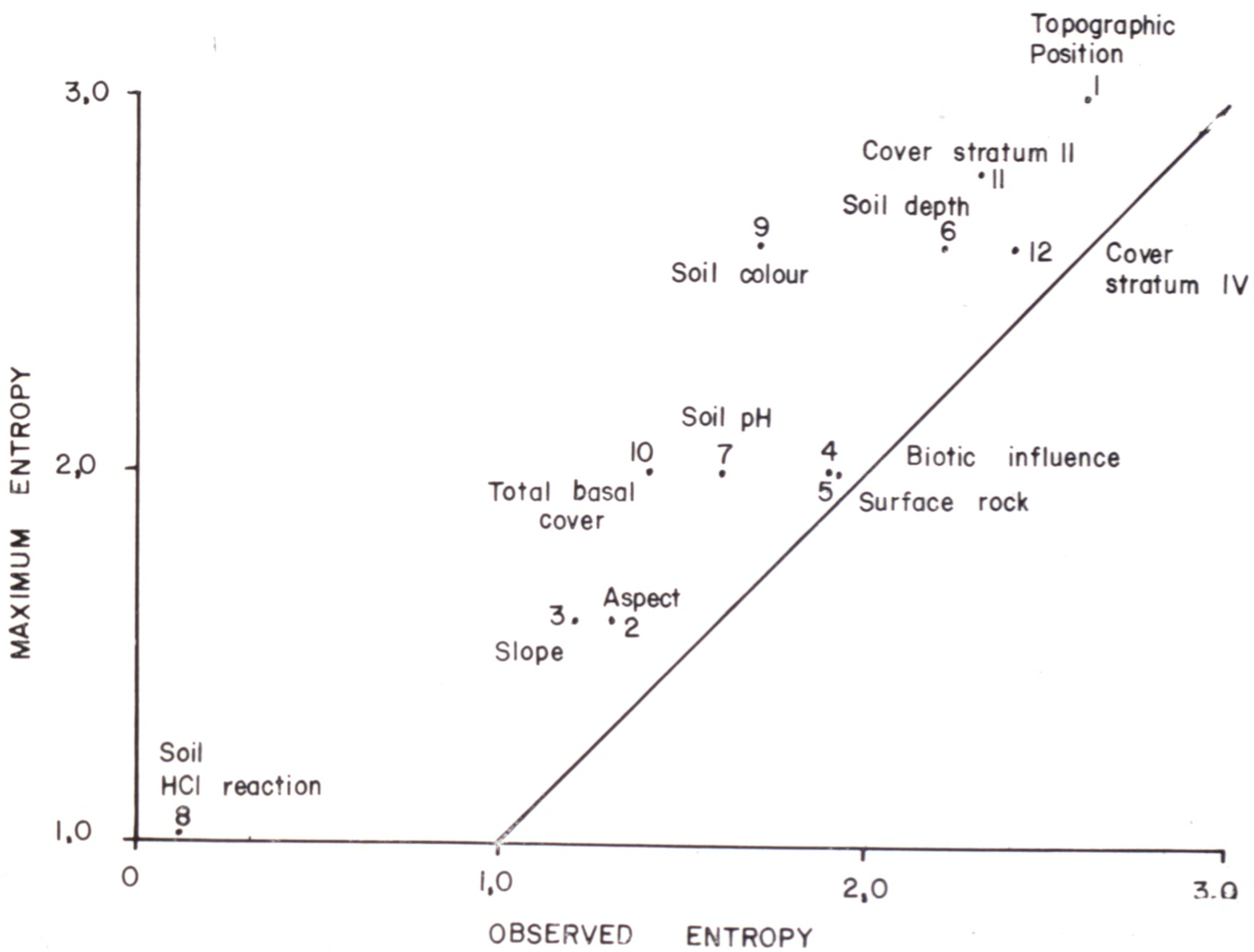

FIG. 1.—Relation between observed and maximum entropy for each ecological variable.

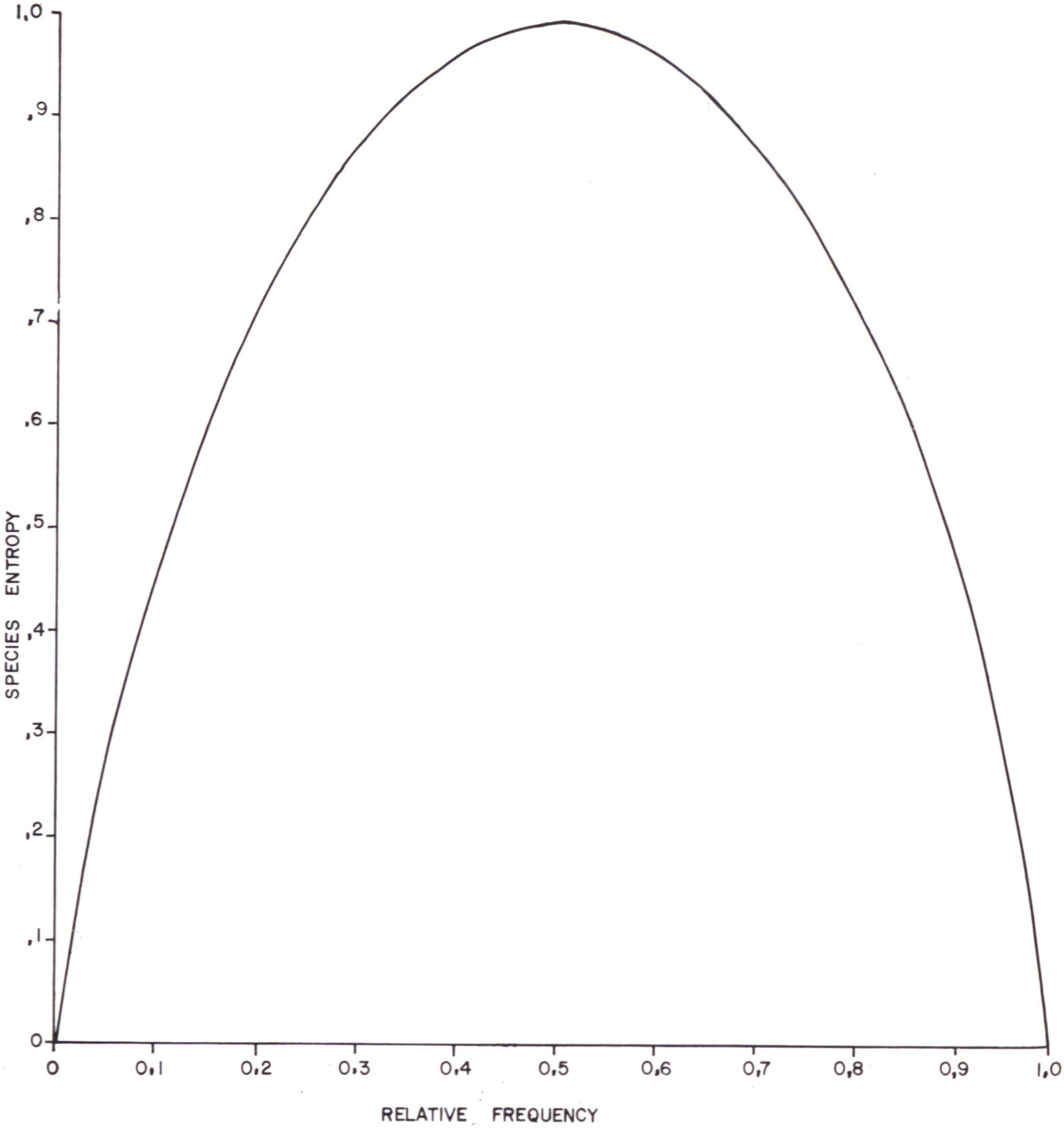

FIG. 2.—Relation between species entropy and relative frequency.

The presences and absences of each species in an ecological profile may be used to calculate species entropy (I_s) which is defined as:

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

where $U_T = \sum_i^K U_i$ and $V_T = \sum_i^K V_i$ (see Table 5)

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 is shown graphically in Fig. 2.

The information carried by a species relative to an environmental variable may be calculated. It is known as the mutual information between species and variable. For species E and variable L (in K classes) it 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 as in Table 5)

As mutual information can be calculated for every species with every variable, a species by variables matrix of entropy values is available. To reduce the volume of results, only certain species and ecological variables are selected, although there is no reason why all the values should not be calculated if this were required.

The calculation of mutual information between species and variables allows the determination of which variables 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 the entropies of the variables. Mean mutual information is plotted along the ordinate and the entropy of the variable along the abscissa to give 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 that variables for re-sampling should be chosen from among those which are insufficiently sampled (to the left of graph) and should be those to which the vegetation appears most sensitive (top of graph). In his application, Godron re-sampled and analyzed twice to obtain a satisfactory sample.

MUTUAL INFORMATION BETWEEN LICHTENBURG SPECIES AND VARIABLES

(a) *Overall relationships*

In Fig. 3 relationships between mean mutual species information 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 229) 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 is a marked positive correlation between mean mutual information and variable entropy, illustrated by the clustering along the 5% line.

The diagonal lines in Fig. 3 give the value of mean mutual information divided by the variable entropy as a percentage. It is an expression of the indicator value of variables.

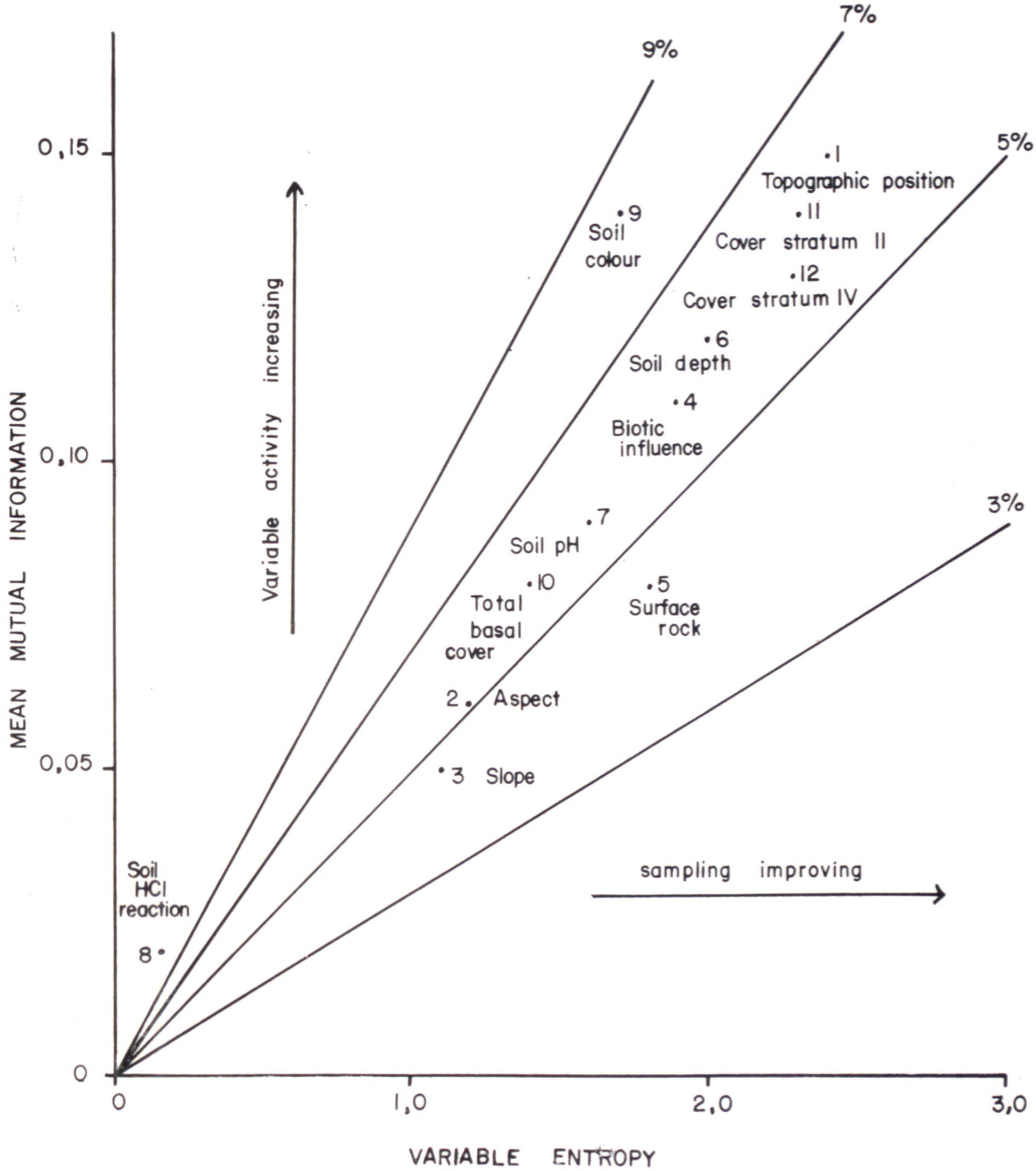

FIG. 3.—Relation between mean mutual information for the species with the highest information content and the entropy of the ecological variables.

The variables are discussed separately in the subsections which follow, but their relationships to each other should not be forgotten; for example, soil depth and biotic influence can be related and soil depth is usually related to slope angle.

(b) *Topographic position*

Profiles for topographic position present difficulties in interpretation even though, as a variable, it is very favourably placed in Fig. 3. Firstly, there is a very asymmetric distribution of quadrats within the classes with class 5 being very poorly sampled (see comprehensive profile, Fig. 4). Secondly, 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 such little relief that large differences in floristic composition related to this variable are not expected. Related to this difficulty is that of the coding of this 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 the field notes.

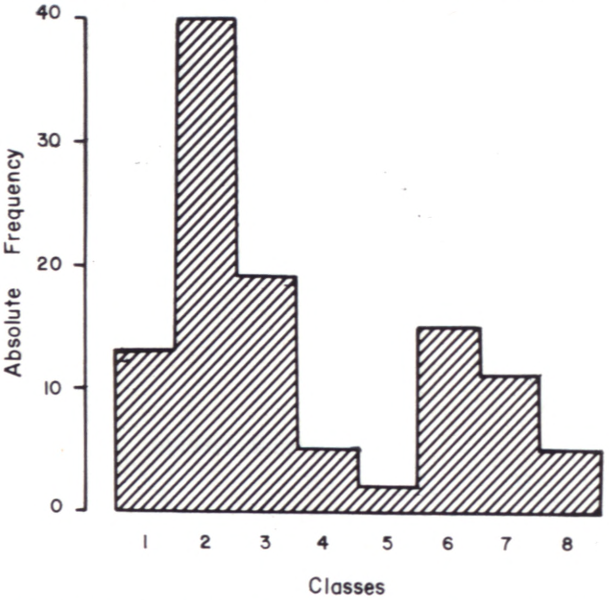

FIG. 4.—Comprehensive profile for the variable topographic position (1=flat, 2=round summit, 3=waxing slope, 4=mid-slope, 5=ledge, 6=waning slope, 7=open depression, 8=closed depression).

At the suggestion of M. Godron (pers. comm., 1973) product-moment correlation coefficients were calculated between each pair of corrected profiles of the 100 species with highest mean mutual information (4 950 calculations) and the 100 highest positive values obtained. 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 correlation values were all significant at p=0,01 % and the first 14 at p=0,001 %. Unfortunately, these values were not as satisfactory as expected since mean mutual information level also has to be taken into account. The following are illustrations. The highest correlation was between *Dicoma anomala* and *Loudetia simplex* that favour flat areas, rounded summits and waxing and waning slopes, according to the 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 importance. 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 are highly correlated, these species occurring mainly on flat areas and in open depressions. As all three have low mean mutual information values, however, the high correlations are again of not much value.

With data specially collected for an ecological profiles study, use of the correlation coefficient to compare species profiles may be of use.

(c) *Aspect*

Aspect was not equitably sampled and is not active in the quadrats (Fig. 3). This 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 synthetic classes were retained. Species favouring flat ground (no aspect) include *Senecio coronatus*, *Gazania krebsiana* and *Nidorella hottentotica*.

Species favouring north and north-west aspects include:

1. *Sporobolus africanus*
2. *Cymbopogon plurinodis*
3. *Eragrostis superba*
4. *Chascanum pinnatifida*
5. *Eragrostis stapfii*
6. *Stipagrostis uniplumis*
7. *Euphorbia pseudotuberosa*
8. *Eragrostis lehmanniana*
9. *Hermannia tomentosa*
10. *Bulbine* sp.
11. *Anthephora pubescens*
12. *Turbina oblongata*

(In the above and following lists, species are ordered by decreasing mutual information content. Figured species have the highest mutual information contents.)

Species favouring the south, south-west, south-east and/or east aspects include:

1. *Dicoma macrocephala*
2. *Diheteropogon amplectens*
3. *Talinum arnottii*
4. *Coleus neochilus*
5. *Trachypogon spicatus*
6. *Blepharis angusta*
7. *Rhynchelytrum repens*
8. *Hypoxis* sp.
9. *Ursinia nana*
10. *Menodora africana*
11. *Pentanisia* sp.

These lists must be considered very 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.

(d) *Biotic influence*

Results which appeared very good were obtained from this environmental variable. The problem with interpreting the results was, however, that the quadrats, as regards biotic influence, were classed on the basis of a subjective appreciation whereby the species composition of the quadrat influenced the assessment of the degree of biotic influence and may have distorted the ecological profiles.

As may be expected, the main patterns of distribution along the biotic influence profile are an increasing or decreasing corrected frequency with increase in biotic influence. Good examples of the former are: *Ursinia nana*, *Eragrostis tricophora*, *Cynodon dactylon* and *E. lehmanniana* (Fig. 5). Other species also having this trend include:

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

A related distribution is shown by *Eragrostis superba*. This species as well as:

1. *Hermannia tomentosa*
2. *Indigofera daleoides*
3. *Chascanum pinnatifida*
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.

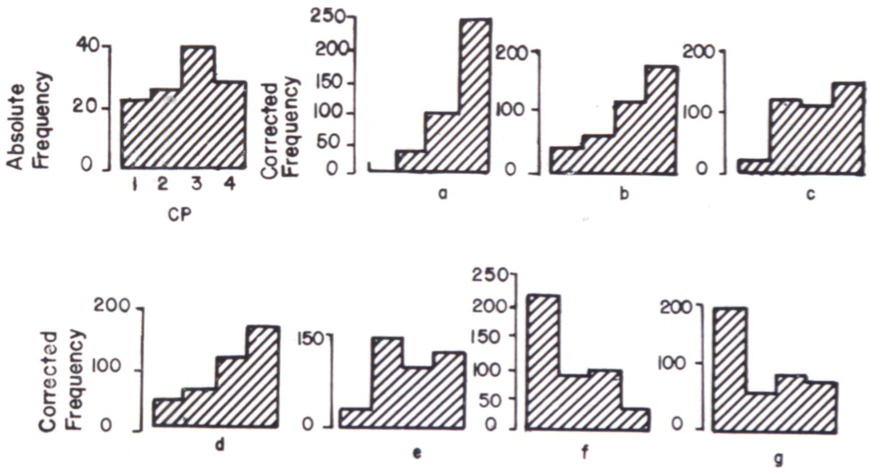

FIG. 5.—Comprehensive profile (CP) and distributions of (a) **Cynodon dactylon,** (b) **Eragrostis tricophora,** (c) **E. lehmanniana,** (d) **Ursinia nana,** (e) **Eragrostis superba,** (f) **Diheteropogon amplectens** and (g) **Clematopsis stanleyi,** representing the two main distributions within the biotic influence profile (Class 1 least influenced, Class 4 most influenced).

Species found on undisturbed areas and having successively lower corrected frequencies as the degree of biotic influence increases, include, notably, *Clematopsis stanleyi* and *Diheteropogon amplectens* (Fig. 5) as well as:

1. *Thesium costatum*
2. *Eragrostis racemosa*
3. *Schizachyrium sanguineum*
4. *Acalypha* sp.
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*

(e) *Soil depth*

The comprehensive profile for soil depth (Fig 6) shows that deeper soils were not well sampled. As the whole study area is a dolomitic lithosol with only pockets of deep soil, additional random sampling will not produce a more even distribution. Equitability of sampling will be achieved only if quadrats are placed at random within the deep-soil pockets.

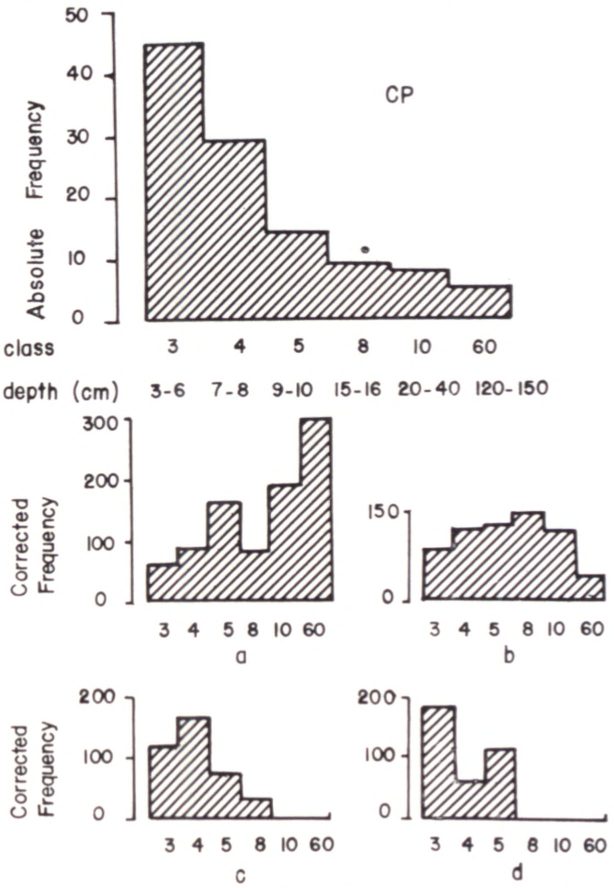

FIG. 6.—Comprehensive profile (CP) and distributions of (a) **Zornia milneana,** (b) **Kohautia omahekensis,** (c) **Ipomoea obscura** var. **fragilis** and (d) **Oropetium capense,** within the soil depth profile.

The ecological profile for *Zornia milneana* (Fig. 6) shows it to occur on deep soil, whereas *Ipomoea obscura* var. *fragilis* and *Oropetium capense* are most frequent on very shallow soil. It was observed during fieldwork that the latter species usually occurred in small sand pockets in extensive dolomite sheets. The profile confirms the observations. 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.

(f) *Soil pH*

Even though this factor was not equitably sampled (Fig. 3), valuable information about the ecology of certain species can be gained from a study of the corrected ecological profiles. Certain species have been plotted in Fig. 7 to illustrate the four main trends.

The most remarkable trend is shown by *Fingerhuthia africana* and *Oropetium capense* (Fig.7), which are restricted to soil with a pH of 8,0 or higher.

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 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. 7). Other species with the same distribution include *Chascanum hederaceum*, *Eragrostis racemosa* and *Sporobolus pectinatus*.

Species found on acid soils but which also grow in neutral pH include *Eragrostis tricophora* and *Dicoma anomala* (Fig. 7). Other species which exhibit this trend of decreasing corrected frequency with increasing pH are:

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

Species showing a peak of corrected frequency in the centre of the range, in other words growing in a neutral or slightly acid soil, include *Barleria macrostegia* and *Lightfootia denticulata* (Fig. 7). Other species with similar distributions include:

1. *Helichrysum caespititium*
2. *Dicoma macrocephala*
3. *Acalypha* sp.
4. *Chaetacanthus costatus*
5. *Diheteropogon amplectens*
6. *Cyphocarpha angustifolia*
7. *Schizachyrium sanguineum*

(g) *Basal cover*

Total basal cover was inadequately sampled (Fig. 3), and is not discussed further. Within the second and fourth strata, however, three patterns of

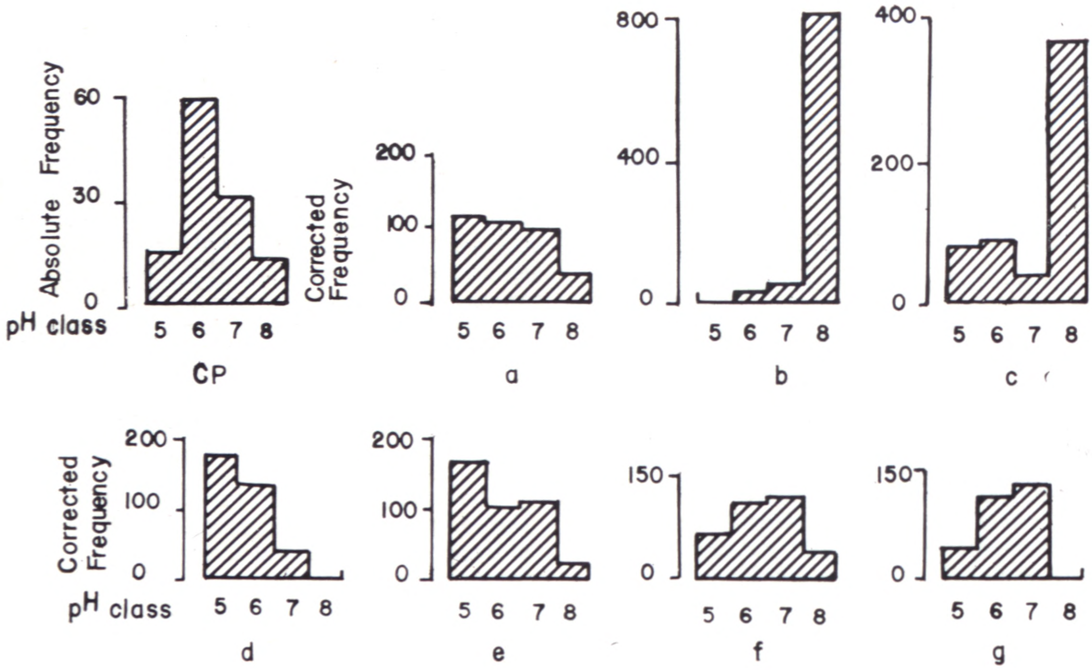

FIG. 7.—Comprehensive profile (CP) and corrected ecological profiles for (a) **Justicia anagaloides,** (b) **Fingerhuthia africana,** (c) **Oropetium capense,** (d) **Eragrostis tricophora,** (e) **Dicoma anomala,** (f) **Barleria macrostegia** and (g) **Lightfootia denticulata,** plotted aginst soil pH classes.

species behaviour emerge. 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. It is stressed that cover is used as an ecological variable and not a structural property of the vegetation. It is assumed that the degree of cover influences the behaviour of certain species.

Species in which peaks of corrected frequency are found in both the second and 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* sp.

Species with peaks in the fourth stratum only, include: *Helichrysum cerastiodes*, *Clematopsis stanleyi* and *Oxygonum dregeanum*.

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

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

In addition to the expected trends described above, certain species show rather odd distributions when both strata are considered. These are illustrated in Fig. 8. *Zornia milneana*, a short, creeping herb

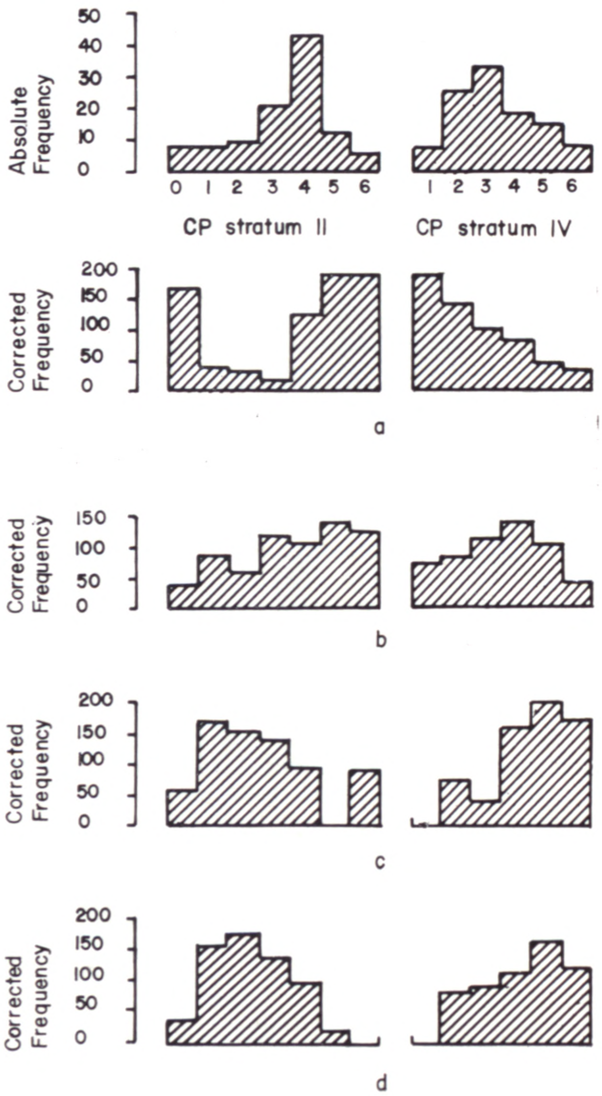

FIG. 8.—Comprehensive profile (CP) and corrected ecological profiles for (a) **Zornia milneana,** (b) **Acalypha** sp., (c) **Diplachne biflora** and (d) **Elephantorrhiza elephantina** plotted against the basal cover classes of the second and fourth strata.

shows a marked J-shaped curve in the second stratum and decreases sharply in the fourth stratum as cover increases. *Acalypha* sp., another short herb, increases in frequency in the second stratum as cover increases but reaches a peak in the fouth 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. 3), inspection of the compreoensive qrofiles (Fig. 8) shows that the distribution of quadrats through the classes is far from regular, which may account for the odd patterns described above.

(h) *Other variables*

Other variables are not discussed in detail. Surface rock is closely correlated with soil depth in this study. As the few slopes within the study area were so gentle, the slope profile does not carry much information. HCl reaction was very poorly sampled and trying to attach ecological significance to soil colour was not considered worthwhile.

SPECIES INDICATOR VALUES

For each ecological variable the species may be ranked by decreasing mutual information content. The rank then gives the species indicator value for that variable. While study of the corrected ecological profiles allows specification of the ecology of the species, it is possible to identify the species of which the ecological requirements are most similar by means of the indicator values. Species with the 20 highest indicator values for each of the 12 variables were listed and species which were listed four or more times are given in Table 6. These species are most active over all the environmental variables.

Instead of looking at the species by variables matrix of mutual information, variable by variable, as was done above, it may be studied species by species. In Table 7 mutual information values of five species are given for the twelve variables. To obtain a

TABLE 6. 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 7.

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 daleoides	*			*		*					*	*	5
13. Ipomoea obscura *var.* 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. Ophrestia retusa	*	*	*						*				4
21. Senecio coronatus		*	*	*		*							4
22. Senecio venosus	*	*	*			*							4
23. Sporobolus africanus		*	*			*	*						4
24. Thesium costatum	*			*	*							*	4
25. Ursinia nana	*			*							*	*	4

TABLE 7. Mutual information between five species and 12 variables (X=mean mutual information, 1=**Stipagrostis uniplumis**, 2=**Schizachyrium sanguineum**, 3=**Turbina oblongata**, 4=**Dicoma macrocephala**, 5=**Justicia anagaloides**).

Variable	X for 1 st 100 species	Species				
		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. Cover stratum II	0,139	0,162	0,172	0,128	0,174	0,168
12. Cover stratum IV	0,129	0,151	0,145	0,137	0,245	0,123

* Not calculated, less than 0,054.

datum, the mean mutual information for the 100 species with highest mutual information values is given for each variable. The relative importance of each species may be obtained by comparing the mean mutual information value with individual values. The five species occurred in one of the first 20 ranked positions of the highest number of variables. Any species in which one was interested could be included. For detailed study of these values it will probably be necessary to use either the species rank or, at least, a corrected value as datum.

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 (pers. comm., 1973) suggested the term 'indicator group'. An indicator group is a collection of species with the same, or similar, ecological requirements. From past work, according to the Daget *et al.*, it appears that the number of groups of species or of isolated species stabilizes rapidly. The succeeding groups confirm those that have been established before, or only modify them slightly. As many variables are usually correlated (for example, slope angle and soil depth) and the active variables are analyzed 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 paper, species that have the same, or a similar pattern of response to a variable have been discussed together, but no attempt has been made to derive indicator groups as the data were considered incomplete.

CONCLUSIONS

For the determination of ecological profiles it is necessary to calculate the entropy, or information content of species, of variables, or 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 a "population" and is treated as such. This equivalence has its limitations in that it assumes the number of quadrats is 'large'. By use of a more complex entropy formula, it is possible, however, to overcome this drawback and use relatively 'small' samples. Experience gained from other analyses carried out at Montpellier shows that, with the entropy formula described above, about 100 quadrats are necessary for a reasonable first approximation. With fewer than 100 quadrats the results should only be used as a guide although the conclusions concerning the necessary improvements to sampling are still useful.

Montpellier ecologists (Daget *et al.*, 1972) stress that the main application of the ecological profiles technique is sampling improvement. Deficiencies in sampling do show up (for example HCl reaction, Figs. 1 & 3), but the ecological profiles produced have another important use. Valuable quantitative, although univariate, information about species reactions to environmental factors is produced. Because of inadequate sampling of habitat variables, the ecological results of the Lichtenburg analysis should be treated with caution although they indicate the potential alue of the technique.

With adequate sampling of habitat 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.

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OPSOMMING

Die metode van ekologiese profiele en inligting verdeel deur spesies en ekologiese veranderlikes, wat in Frankryk ontwikkel is, word vir die eerste keer in Engels beskryf. Voorlopige resultate van die gebruik van die tegniek op gegewens in die Bankenveld van Lichtenburg in Wes-Transvaal, word gegee. Ten slotte word genoem dat dié metode 'n groot potensiële bydrae kan lewer tot die begrip van die outekologie van Suid-Afrikaanse spesies, mits monsterneming by dié tipe van analiese aangepas word.

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