Cape Hangklip area. I. The application of association-analysis, homogeneity functions and Braun-Blanquet techniques in the description of south-western Cape vegetation

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ABSTRACT

Relevé data were collected in two phases from, respectively 150 and 100 sampling points distributed by stratified random means through almost 24 000 ha of vegetation. Association-analysis, Braun-Blanquet and homogeneity function methods were used to treat the data. Only the "normal" association-analysis method was applied. Three sorting techniques for tabulating the data were tested and were compared with a fourth method. Homogeneity functions were used to construct a dendrogram and to determine the degree of similarity between individual relevés and groups of relevés. After comparison of the methods, it was concluded that the Braun-Blanquet method is consistently more efficient and more exact, even in the floristically rich vegetation of the south-western Cape Province of South Africa.

INTRODUCTION

Little descriptive work has been done on the vegetation of the south-western Cape Province of South Africa. Accoks (1953) has remarked that the Cape Fynbos vegetation "is a complex vegetation, and to divide it simply into Macchia and False Macchia is like dividing the tropical vegetation into grassveld and bushveld ...." Statistical approaches have been used by Rycroft (1951), Grobler (1964), Taylor (1969) and Hall (1970) as aids in the description of this vegetation. The largest area of vegetation described and mapped in detail is the 7 680 ha of the Cape of Good Hope Nature Reserve (Taylor, 1969). This latter study was the first attempt at applying association-analysis (Williams & Lambert, 1959, 1960, 1961; Lambert and Williams, 1962) and Zürich-Montpellier methods (Braun-Blanquet, 1932; Becking, 1957; Küchler, 1967) to the Fynbos element (Taylor, 1972) of the South Western Cape vegetation. The Zürich-Montpellier principles, expressed by Braun-Blanquet and further developed theoretically by many followers (Weger, 1973b), will here be termed the Braun-Blanquet method. The Braun-Blanquet method has subsequently been used to describe some 373 ha of Fynbos vegetation in the Jonkershoek State Forest near Stellenbosch (Weger, Kruger & Taylor, 1972).

A method was required in the south-western Cape that would be most suitable for the evaluation, description and classification of large tracts of Fynbos vegetation. The Cape Hangklip area was floristically rich and included many variations of habitat. It would, therefore, be an exacting test of the suitability of any method. This served as the stimulus to apply homogeneity functions (Hall, 1967a & b, 1969a, b & c and 1970), association-analysis and Braun-Blanquet techniques.

The study area consists of about 24 000 ha of coast and mountain vegetation. The boundaries were taken as those of the 1:50 000 Topographical Survey Sheet 3418BD Hangklip (Trigonometrical Survey, 1968) and the portions of the Kogelberg State Forest which occur outside this sheet.

METHODS

The sampling method

Relevé data were obtained from 150 and 100 sites scattered respectively over 11 506 and 12 354 ha. Sites were distributed randomly within physiographic-physiognomic units delimited on aerial photographs. In the first phase of 150 relevés, each of the 10 x 5 m relevés were strictly laid out with the longest axis on a north-south magnetic bearing. In the second phase each of the 100 relevés was so positioned that a maximum of 24 000 ha of vegetation. The method was applied. Three sorting techniques for tabulating the data were tested and were compared with a fourth method. Homogeneity functions were used to construct a dendrogram and to determine the degree of similarity between individual relevés and groups of relevés. After comparison of the methods, it was concluded that the Braun-Blanquet method is consistently more efficient and more exact, even in the floristically rich vegetation of the south-western Cape Province of South Africa.

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The following additional information was recorded at each sampling site: soil type, soil moisture, degree and type of stoniness, local climatic data, geology, geomorphology, species dominance, species height, vegetation age, disturbances, etc.

The association-analysis method

The various forms of association-analysis, namely, "normal", "inverse" and "nodal" analyses, have been fully described by the developers of the method and by numerous other workers. South African workers who have applied this method include Van der Walt (1962), Grunow (1965), Downing (1966), Roberts (1966), Woods & Moll (1967), Miller & Booyzen (1968), Scheepers (1969) and Taylor (1969).

Scheepers (1969) found that the inverse analysis produced a stepwise arrangement of species grouping (also known as "chaining") which was difficult to interpret. Morris (pers. comm.) considered this stepwise arrangement to be a fairly regular feature of the method when large numbers of species were involved, as in this case. It was considered advisable to restrict treatment of the data to the normal type of analysis. Information gained from inverse and nodal analyses would, in most instances, not warrant the extra expenditure in computer time. A programme for the nodal analysis was not locally available at the time.

The subdivision parameter used was the highest value which Williams and Lambert (1959, 1960) considered to result in the most efficient subdivision, although the optional facilities of $\Sigma x^2$ or $\Sigma x^2/N$ were available. Termination of subdivision took place when there were less than eight relevés left in the group or when the highest single $x^2$ equalled 3,841 or less.

The Braun-Blanquet method

The Braun-Blanquet method, commonly used in Europe and elsewhere, has been little used in South Africa. The only English source of information on this method was Fuller and Conard's (Braun-Blanquet, 1932) authorized translation of Braun-Blanquet's first edition of Pflanzensoziologie (Braun-Blanquet, 1928). More recent English descriptions of the method were published by Poore (1955), Becking (1957) and Küchler (1967), amongst others.

Taylor (1969) was the first to use the method in South Africa. He prepared a synthesis table from data collected in systematically distributed relevés and obtained associations which were recognizable in the field. Werger, Kruger & Taylor (1972) then applied the phytosociological technique as further described by Ellenberg (1956) and Braun-Blanquet (1964), to test its usefulness in the floristically rich Fynbos vegetation in a portion of the Jonkershoek State Forest. A practical classification into communities based on floristic criteria was obtained. This method has subsequently been used by, amongst others, Coetzee (1972) in the Jack Scott Nature Reserve, by Werger (1973a & b) in the Upper Orange River Valley, and by Musil, Grunow & Bornman (1973) on aquatic vegetation in the Pongola Pans, Zululand.

Aids have recently been developed to assist in sorting tabulated data. Müller et al. (1972) designed a mechanical sorting apparatus for ordering data by shifting aluminum strips on which the information is symbolized by coloured rivets. A computer programme, TABSORT, developed by the Department of Forestry at Jonkershoek near Stellenbosch, allows the data matrix to be manipulated simply by listing the relevé and species sequences in the required new order. Ceska and Roemer (1971) have developed a computer programme that identifies species-relevé groups in vegetation, thereby removing the much disputed personal bias from table-work.

Method using homogeneity functions

Homogeneity functions for identifying groups in a matrix of vegetation data have been developed by Hall (1967a & b, 1969a, b & c and 1970). A function, given as $H_{em}$, is written for the subset of $t=1 \ldots k$ sample plots and all the $j=1 \ldots p$ species, as follows:

$$H_{em} = \sum_{j=1}^{p} \frac{a_{jt}}{\sigma_j^2} \left( 1 - \frac{s_{aj}}{s_{aj}} \right)$$

where $s_{aj}$ and $s_{aj}$ are the standard deviations of the subset's actual data row for the $j$th species, and a dummy maximally heterogeneous row, respectively; $a_{jt}$ is the value for the $j$th species in sample plot $t$. These methods have only been tested on small vegetation data matrices from the Bains Kloof area of the Cape Province. A simplified form of this homogeneity function determines the similarity between the average members of each major group, subgroup, sibling-group (Hall, 1969a) or core and each relevé, thereby indicating the "goodness of fit" of each relevé in each vegetation group delimited.

The similarity between two items or average members $t$ and $k$ can be given by this simplified version of the homogeneity function. By similar notation,

$$H_{em} = \sum_{j=1}^{p} \frac{M_j \left| a_j - \bar{a}_j \right|}{\sigma_j^2}$$

Here, the modulating factor $M_j$ is calculated exactly as before. The homogeneity expression that follows, uses abundance values scaled to a range with a maximum of one, $a_j$ and $\bar{a}_j$. The scaling of the $j$th species is based on its largest operational value (Hall, 1970).

RESULTS AND DISCUSSION

Association-analysis

For practical reasons collection and treatment of the data were divided into two separate phases.
Fig. 1.—First-phase association-analysis hierarchy from Boucher (1972).
ASSOCIATION - ANALYSIS HIERARCHY
SECOND PHASE

LEGEND
x and o indicate presence or absence of dividing species
17 indicates number of sample plots in subdivision

Fig. 2.—Second-phase association-analysis hierarchy.
Fig. 3.—Homogeneity-function dendrogram from Boucher (1972).
In the first phase, 150 relevés were ordered into 32 final groups in the association-analysis hierarchy (Fig. 1). The hierarchy was constructed following the conventional procedure of listing positively defined relevés at each subdivision, on the left-hand limbs and the negatively defined relevés on the right-hand limbs. To present the information in a more practical fashion, a logarithmic, instead of a linear scale, was used for values of highest single $x^2$. The linear representations are inset in Figs 1 and 2.

The hierarchy showed relatively uniform divisions with little tendency to chaining, except in the final negatively associated portion, where the more distinctive communities such as the coastal dune vegetation and wet seepage communities, occurred. A reversal, or increase, in level of subdivision of a subsequent group, following the removal of a more homogeneous group, occurred after group 12 had been delimited. In certain instances, such as in the subdivision of groups six and seven, two species could equally well have been used to effect the subdivision, both resulting in the smallest total of residual significant associations in the two resulting subclasses. When such an ambiguity occurred, the computer was instructed to subdivide on the species with the lowest coding number.

In most cases communities proved to be understood and sampled in a manner that very few instances would the recombination of adjacent final groups have resulted in ecologically valid larger groups.

A major difficulty, probably more commonly found in monothetic divisive techniques was the occurrence of apparent misclassifications. These were found especially during the first major subdivisions when large numbers of relevés were involved. Here the chance absence of a species within a particular relevé, although it occurred within the community being sampled, could result in the misclassification of a relevé. This contingency was largely overcome by listing species not found inside the relevé but occurring in its immediate vicinity, within the same community. The reclassification of any relevé could be undertaken on these grounds. In a number of instances the cause was found to be the misidentification of the dividing species. This was attributed to the drought conditions prevailing at the time and to the problem of identifying vegetative specimens. The collection of 114 species of Ericaceae, characterized by ericoid leaves, underlines the reality of this problem. More than 1400 different species complement in each relevé. A relationship of a different type, such as fire-age, might be indicated. This is possible when the grouping is based on total species complement in each relevé. A relationship of a different type, such as fire-age, might be indicated. This detracts from the acceptance of the association-analysis, in comparison to the Braun-Blanquet, groups for community classification.

Homogeneity functions

The initial subdivision of the data before applying homogeneity functions was done using the Braun-Blanquet method. The easily extractable, obvious groups were accepted prior to being further analyzed using homogeneity functions. The residual data matrix consisted of 108 relevés having 185 permanently recognizable species occurring in more than two relevés. This matrix was still too large for analysis by this method with the available computer facilities. It was, therefore, further reduced by excluding the species of less frequent occurrence until 86 species remained.

A chaining effect was obtained in the homogeneity function dendrogram (Fig. 3) with virtually no distinct clustering. A broad moisture gradient could be discerned in the arrangement with drier sites linking onto the matrix at the higher homogeneity
levels and wetter sites linking at the lower homogeneity levels. This was similar to the association-analysis grouping wet seepage communities linked at the lower highest single $\chi^2$ values.

The data matrix for comparison using the homogeneity functions consisted of the less distinct communities. The absence of the species of rarer occurrence probably reduced the sensitivity of the method to an excessive degree. The end product was, therefore, unsuitable for the description or the mapping of the vegetation.

The distinctness of the recognized groups, and of the members in each group, to their average member was determined using the simplified form of the homogeneity function. With this method a member, when compared to itself, would be 100% similar. All the groups recognized were compared to each other, whether they were those delimited by the Braun-Blanquet method or were indifferent groups or arbitrary cores extracted from the homogeneity function dendrogram. The distinctness of the Braun-Blanquet groups was confirmed (vide the example in Fig. 4, where the length of the bar indicates the degree of similarity). The degree of similarity between the relevés in the complex data matrix was also readily shown diagrammatically by the length of the bars.

Affinities between groups and the best location of transitional relevés are easily shown by this method.

CONCLUSIONS

The relevé size (10 m x 5 m) was found to result in an adequate sample of each community, at the scale of study involved. The relevé shape could possibly have been more flexible, for instance in sampling the riparian communities which form narrow bands along streams. The less rigid sampling arrangement of the second phase, where the relevé was not placed in a fixed direction, but in a position to ensure maximum homogeneity, resulted in fewer transitions being sampled and thereby proved to be more satisfactory.

Although the mechanical table sorter was not used to re-arrange the data during this study, experience in its use indicates that it has certain advantages and disadvantages over the TABSORT programme. It is quicker to compare relevés with one another and with developing groups with the mechanical table sorter, because direct comparisons are possible. This is most easily simulated with the TABSORT programme by strip-cutting the data, although this can be tedious and liable to error. Copies of new arrangements must frequently be made. The TABSORT programme has the advantage of providing an immediate neatly typed transcript of the data matrix (150 x 363) was not limited by the computer capacity during this study but rather by the number of relevés and species which could be efficiently dealt with in the actual arrangement. The mechanical table sorting method is more liable to human transcript errors. The size of the data matrix (150 x 363) was limited by practical design and ease of handling (124 x 130 in the prototype).

Taylor found that association-analysis revealed groups which were ecologically meaningful, but that most of the groups represented "such small isolated fragments of natural units that they do not give a harmonious picture of the vegetation" (Taylor, 1969). In the first phase of the Hangklip survey, the ecologically meaningful groups required little subjective ordering to form a more harmonious picture of natural units. The groups in the second phase were found, in contrast, to represent isolated fragments which would require considerable subjective rearrangement. This was in agreement with Taylor's findings. The latter result was unexpected, because care had been taken to ensure the most efficient sampling.

The Braun-Blanquet method was found to be more consistent, primarily because the communities are better defined in that they do not depend on single species presence or absence for final group forming. In addition the relationship between the communities is readily demonstrated. Donselaar who used the Braun-Blanquet method in the savannas of Northern Surinam is mentioned by Werget et al. (1972) as stating that the number of species must be moderate for this method to be successful. The latter workers, in contrast, found the method to be practical in floristically rich fynbos vegetation. During the present study more than 1 400 different species were collected. In the first phase relevés containing 365 species (species occurring in fewer than three or less relevés were not included in the analysis) were satisfactorily ordered in a table. This method, therefore, proved satisfactory with a fairly large data matrix. The data matrix, in contrast, proved to be too large for analysis using homogeneity functions. Initial Braun-Blanquet groups had to be defined prior to further analysis. The homogeneity function tests on these groups showed them to be reasonable. Little further subdivision of these groups using homogeneity functions was effected although the degree of similarity between individual members and groups was readily demonstrated.

The Ceska & Roemer programme for identifying species-relevé groups only resulted in the delimitation of the major groups which were readily delimited using less sophisticated and cheaper facilities.

ACKNOWLEDGEMENTS

The research undertaken during the first phase was submitted to the University of Cape Town for a M.Sc. degree under Dr A. V. Hall.

The Secretary of the Department of Forestry gave permission for data to be collected in a State Forest.

Considerable assistance was received from staff members of the Botanical Research Institute, the University of Stellenbosch, the Department of Forestry at Jonkershoek and the University of Cape Town.

UITTREKSLE

Monsterverseadelaar is versamel in twee fases van 150 en 100 elk, versprei deur byna 24 000 ha plantegroei. Assosiasie-analise, Braun-Blanquet en homogeniteitsfunksie metodes is op die data getoets. Slegs die "normale" assosiasie-analise metode is toegepas. Drie metodes van datasortering vir tabulerings getoeens en is vergelyk met 'n vierde metode. Homogeniteitsfunkstes is gebruik om 'n dendrogram op te trek en om die graad van ooreenkoms tussen die individuele monsterpersele en groep daarvan te bepaal. Die verskillende metodes word vergelyk. Die Braun-Blanquet metode is gereeld meer doeltreffend en presies as die ander metodes getoeens in die floristies ritk plantegroei van die Suidwes Kaap Provinsie van Suid-Afrika.

REFERENCES


Note. The group similarity determinations were undertaken on percentage similarity.

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Fig. 4.—Group similarity analysis from Boucher (1972).


A preliminary account of aerial plant biomass in fynbos communities of the Mediterranean-type climate zone of the Cape Province

F. J. KRUGER*

ABSTRACT

Aerial plant biomass has been sampled by harvesting on several sites in fynbos communities of the southwestern Cape Province.

Biomass in stands of about two years old ranged from about 2 200 kg per ha to about 7 500 kg per ha. Mature stands comprised about 11 000 to 15 000 kg per ha in heaths and 15 000 to 26 000 kg per ha in sclerophyllous scrub. The data indicate a maximum annual growth rate of 1 000 to 4 000 kg per ha early in the development of a stand, but growth rates appear to decline rapidly as communities age.

Young stands are dominated by hemicryptophytes, which comprise about 2 000 to 6 000 kg per ha, or about 60 to 75 per cent of the biomass in stands of about four years old. Shrubs become prominent later, but the hemicryptophytes persist.

The data indicate that the biomass, growth rates and the shape of the growth curves of fynbos communities are on the whole similar to those of analogous vegetation in other zones of Mediterranean-type climate. However, there are important structural differences in that analogues of the northern hemisphere (garrigue, chaparral) do not have a significant component of persistent hemicryptophytes. Although Australian heath communities do have this feature, the hemicryptophytes are not as prominent as in fynbos.

INTRODUCTION

The ecology of natural communities of Mediterranean-type ecosystems has recently received considerable attention, particularly from the point of view of ecosystem convergence, and much more information on plant communities has become available (Specht, Rayson & Jackman, 1958, and previous papers; Specht, 1969a, 1969b; Jones et al., 1969; Mooney et al., 1970; di Castri & Mooney, 1973). However, few data on the Cape fynbos have reached the press.

In this paper data have been collated on the biomass of fynbos communities, which have become available during the course of ecological studies from 1967 to 1974. The studies were not aimed at measuring community production nor are the data such that they may be used as direct measures of productivity. Nevertheless, they represent an index of productivity and contain other useful information.

STUDY AREAS

Biomass surveys were conducted on various sites in three research areas, each described below.

1. Jonkershoek Forest Research Station (sites 1.1-1.4). The research area at Jonkershoek is situated at about 33°57'S and 18°55'E. The ecosystem has been described by Wicht et al. (1969). The communities sampled are situated on the slopes and near the bottom of a steep-walled valley (Fig. 1) and occur on soils derived from Cape granites. Soils are about one metre deep with a brown structureless A-horizon on a yellow-brown apedal B. They are acid, with pH ranging from about 4.50 to 5.00. Extractable phosphorus (citric acid extract) amounts to about 12 to 40 p.p.m. and total nitrogen and organic carbon content amount to 0.1 to 0.2 per cent and three to eight per cent respectively, in the A-horizon (Joubert, 1965).

2. Zachariashoek Research Catchment (sites 2.1-2.3). This catchment research area is situated at 34°49'S and 19°02'E and has been described by van der Zel (1974). The communities studied are situated in the Kasteelkloof subcatchment (Fig. 2). Soils are derived from sedimentary orthoquartzites and shales of the paleozoic Table Mountain Group. The soils here have not been studied, but would resemble those at Jakkalsrivier rather than those at Jonkershoek. Site 2.2 is phreatic and the soil has an organic A-horizon.

Few climatic data are available. Rainfall at the top of the catchment amounts to about 1 300 mm per annum, and at the bottom, 1 100 mm per annum (six-year records at 707 mm and 274 mm respectively).

3. Jakkalsrivier Research Catchment (sites 3.1-3.10). Plathe & van der Zel (1969) and Kruger (1974) have described the Jakkalsrivier area in some detail (Fig.
A PRELIMINARY ACCOUNT OF AERIAL PLANT BIOMASS IN FYNBOS COMMUNITIES OF THE MEDITERRANEAN-TYPE CLIMATE ZONE OF THE CAPE PROVINCE

Fig. 1.—View of sclerophyllous scrub community at site 1.2, Jonkershoek, shortly after sampling. Prominent shrubs are *Rhus tomentosa* and *Anthospermum aethiopicum*. *Asteraceae* dominate the lower shrub stratum.

Fig. 2.—View of open sclerophyllous scrub community at Zachariaeshoek (site 2.1) at age five years. Here, the sclerophyllous shrubs have not yet emerged and the community is dominated by *Restionaceae*: *Chondrostephion paniculatum*, *Hypodiscus argenteus* and *Cannomois virgata* are prominent.

Fig. 3.—View of microphyllous evergreen dwarf scrub (low heath) community at Jakkalsrivier (site 3.7), at age 14 years. The shrub stratum is dominated by *Erica hispidula*.