

# On concepts and techniques applied in the Zürich-Montpellier method of vegetation survey

M. J. A. WERGER \*

## ABSTRACT

Because a wider use of the Zürich-Montpellier method in the study of vegetation in South Africa is envisaged, an outline of concepts and techniques applied in that method is given.

## TABLE OF CONTENTS

	<i>page</i>
Introduction.....	309
1. Sampling.....	310
1.1 Site selection.....	310
1.2 Representativeness.....	310
1.3 Homogeneity.....	310
1.4 Minimal area and plot size; plot form	311
1.5 Structure.....	312
1.6 Floristic lists.....	313
1.7 Cover-abundance.....	313
1.8 Sociability.....	314
1.9 Other analytic characters of the vegeta- tion.....	314
1.10 Habitat characteristics.....	314
1.11 Relevé.....	315
1.12 Number of relevés.....	315
2. Synthesis.....	315
2.1 Tabulation.....	315
2.2 Synthetic characters, character species, differential species.....	316
2.3 Ecological confirmation of the table pattern.....	317
2.4 The association and other syntaxa; the constancy table.....	317
2.5 Nomenclature.....	318
2.6 Homotoneity; affinities between syntaxa	318
2.7 Community structure.....	319
Acknowledgements.....	320
Opsomming.....	320
References.....	320

## INTRODUCTION

The science of plant ecology has been practised in South Africa since the beginning of the present century. Of the early ecological studies in South Africa, the comprehensive treatise on the vegetation of the Cape Province by Marloth (1908) is perhaps the most significant. For more than half a century thereafter South African ecology was predominantly inspired by the writings of Clements (e.g. Bews, 1918; Phillips, 1931; Bayer, 1955; Killick, 1963) and Tansley (e.g. Adamson, 1938; Story, 1952; Edwards, 1957). The studies of this period, discussed in more detail by Killick (1967), were mainly of a non-formal, descriptive nature and often admirably accurate and informative. During the early fifties two ecological studies were of considerable local significance. In 1953 Acocks published his "Veld Types of South Africa", a classification of South African vegetation into 70 veld types and 75 variations, based on a floristic comparison of stand data. Acocks selected well-developed, extensive patches of vegetation and recorded all species encountered. Abundance of each species in each stand was estimated and from comparison of these lists the veld types were

extracted. Since its publication, Acocks' Veld Types has formed the basis of the majority of ecological studies carried out in South Africa. In 1955 Tidmarsh & Havenga published their statistical wheelpoint method for surveying and measuring the cover of vegetation, which has since been used extensively in Southern Africa in its original as well as in modified forms.

The development of statistical techniques in ecology received attention in South Africa soon after the introduction of these techniques in Europe and America and, mainly from 1960 onwards, several studies were undertaken using Goodall's (1953) interspecific correlation analysis (Van Vuuren, 1961), association analysis (e.g. Grunow, 1965; Roberts, 1966; Scheepers 1969; Taylor, 1969; Coetzee, 1972), information analysis (Grunow & Lance, 1969), hierarchical syndrome analysis (Coetzee & Werger, 1973) and various kinds of ordination techniques (e.g. Woods & Moll, 1967; Morris, 1969; Moll, 1969; Grunow & Morris, 1969; Louw, 1970).

The Zürich-Montpellier or Braun-Blanquet approach to the study of vegetation has, since its origin in Europe shortly after the turn of the century, proved to be an efficient and reliable method for vegetation survey and classification in most countries of Europe and also in other continents (Whittaker, 1962; Braun-Blanquet, 1968; Tüxen, 1969, 1970a; Doing, 1970). However, until 1969 this approach remained virtually unknown in Africa south of the equator, except for work in Zaïre, Rwanda and Burundi by Belgian phytosociologists, a vegetation survey in southern Mocambique by Myre (1960, 1962, 1964), and a small survey in the Windhoek area of South West Africa by Volk & Leippert (1971) (cf. Werger, 1973a; Werger *et al.*, 1972). Language difficulties, amongst others, were suggested as a main reason for this remarkable omission by Werger *et al.* (1972). But basic differences between the scientific approaches of Anglo-American and continental European ecologists should also not be underestimated. Although English accounts of several aspects of the method were given by Braun-Blanquet as early as 1932, and later by Poore (1955, 1956), Becking (1957), Moore (1962) and later authors, lack of training as well as the local psychological climate that was by then so influenced by the attitude of general non-acceptance of the method, prevailing amongst the English-speaking ecologists, prevented its application until 1969. In 1969 a phytosociological survey of the Upper Orange River valley, in which the Zürich-Montpellier method was applied, was initiated (Werger, 1973a) and since then a number of smaller surveys, in which this method was successfully applied, were carried out (Van Zinderen Bakker, 1971; Werger *et al.*, 1972; Werger, 1973b; Leistner & Werger 1973; Van Zinderen Bakker & Werger, 1973; Coetzee, 1974; Coetzee & Werger, 1974). Because of the success of these studies a wider acceptance of the Zürich-

\* Botanical Research Institute, Department of Agricultural Technical Services, Private Bag X101, Pretoria; now at: Botanisch Laboratorium, Afd. Geobotanie, Toernooiveld, Nijmegen, Netherlands.

Montpellier method in South Africa is envisaged. A discussion of the concepts and techniques applied in this method, particularly of those aspects not covered by the previously-mentioned as well as the more recent publications in English (Küchler, 1971; Shimwell, 1971), was therefore thought to be useful. In this presentation no pretence to completeness is made.

According to the Zürich-Montpellier method, selected, representative, homogeneous plots of a certain minimum size are sampled in the phytocoenoses (stands) making up the vegetation of the area to be surveyed, recording all species and rating them on a cover-abundance and, optionally, a sociability scale. Some other analytical characters of the vegetation in the plot might also be recorded. The samples are entered in a table from which the vegetation units are extracted. The units are interpreted ecologically and ranked in a hierarchy. Thus, the method consists of an analytical, sampling phase and a synthetic phase, which will be discussed separately.

## 1. SAMPLING

### 1.1 Site selection

In the Zürich-Montpellier School the selection of a site for a plot is generally carried out subjectively. Although much and severely criticized, this procedure is in accordance with the community-unit theory, which postulates that vegetation consists of natural entities usually in contact with each other along narrow boundaries (cf. Werger, 1973a; Whittaker, 1956, 1962, 1967). The most efficient way to find the units or associations, which are types abstracted from actually-occurring stands or phytocoenoses, is to select for sampling those stands which may possibly be examples of such an association. Stands which are obviously heterogeneous in habitat, structure or floristic composition, and might therefore logically be expected to represent parts of two or more units or associations, should be avoided because they do not contribute information which can be used to describe the two or more community-types that they represent. Thus, the subjective decision to avoid mixed stands does not imply the circularity suggested by Whittaker (1956): "associations are being studied in terms of samples taken in terms of associations". The real procedure is that associations are being studied in terms of plot samples taken in terms of phytocoenoses which are possible association-individuals. It is obvious that the question of subjective selection of phytocoenoses for sampling is closely related to the question of representativeness, homogeneity and total number of plots to be sampled. The area of investigation must be well known in all its variety before the study is started, since a good knowledge of the variation in the study area allows a more representative sampling of the various stands (phytocoenoses). Prejudice about the expected results of the study should be avoided in this selection. The subjective selection of stands for sampling, guarantees an optimal sampling efficiency, because obviously heterogeneous plots are avoided as far as possible (Ellenberg, 1956; Becking, 1957; Dahl 1957; Barkman, 1958; Gounot, 1961, 1969; Braun-Blanquet, 1964; Daubenmire, 1968; Moore *et al.*, 1970; Knapp, 1971). The strength of the arguments against the procedure of subjective selection of plot sites is often overestimated, since it seems to be difficult, according to the experience of Ivimey-Cook & Proctor (1966) to "collect any substantial body of phytosociological data to support a conclusion seriously at variance with the facts". On the other hand, this question need not be crucial in the decision to apply the Zürich-Montpellier method, since there is no fundamental objection

against stratified random, random and systematic sampling. These sampling strategies can also yield good results. Particularly in the last two cases, however, a considerable amount of plot data will be too heterogeneous to be used in the extraction of community-types (cf. Taylor, 1969). A test for homogeneity of the plots might prove useful when these strategies are used. When they are used in an area where different communities occur in a mosaic of patches of small dimensions, the possibility exists that virtually no plot may be usable, or that so many plots are situated on similar transitions that these transitions are also extracted from the tables and can wrongly be interpreted as types. Great care should thus be taken in evaluating the plot data and the synthetic results based on random and systematic sampling strategies.

### 1.2 Representativeness

Stands for sampling should be selected in such a manner that each is representative of the vegetation of which it is part and that each plot sampled therein should yield a more or less typical description of that vegetation in terms of both floristic composition and structure. Each plot should represent only one entity of vegetation (Ellenberg, 1956; Dahl, 1957; Gounot, 1961; Braun-Blanquet, 1964; Knapp, 1971). In an open tree or shrub vegetation, for example, the situation of plots should be such that the relative importance of the tree or shrub component within the plot is comparable with that of the surrounding vegetation to be represented.

The requirement of representativeness of the vegetation in the sample plot should not be confused with the question of the degree of development or disturbance of the vegetation. Although samples taken in optimally developed vegetation are most suitable for the first description of a new syntaxon (Westhoff, 1967, 1968; Westhoff & Den Held, 1969), it will often be useful to sample stands representative of below-optimally developed vegetation, such as overgrazed grassland. Such a sample is important in the establishing of the status of the grassland concerned and of the successional trends under the influence of a specific treatment of the vegetation to which the sample belongs. When random or systematic sampling is carried out, the question of the representativeness of each individual plot is, of course, by-passed. This disadvantage is particularly important in open vegetation.

The representativeness of a plot is closely related to its homogeneity.

### 1.3 Homogeneity

According to Goodall (1952), "homogeneity has bulked large in ecological literature, because most schools of plant sociology specify it as a first desideratum for a 'stand' or area of vegetation, which can serve as a unit of classification".

The approaches based on the community-unit theory and those based on the individualistic hypotheses both require homogeneous sample plots (Bray & Curtis, 1957; Curtis, 1959; Grunow & Morris, 1969). Workers using the various ordination techniques often assess only floristic homogeneity of the sample plot, relating homogeneity to the distribution of the species present in the sample plot. In the Zürich-Montpellier School floristic, structural and environmental homogeneity are usually assessed visually. Homogeneity is important in the community-unit theory approaches because information per sample of one vegetation entity only, and not of mixtures, is wanted (Ellenberg, 1956; Dahl, 1957; Barkman, 1958; Gounot, 1961, 1969; Braun-Blanquet, 1964; Daubenmire, 1968; Tüxen, 1970b; Knapp, 1971;

Shimwell, 1971). Most techniques for testing homogeneity of the sample plot start tacitly from one of two assumptions; either that if the plot is floristically homogeneous it is also structurally and environmentally homogeneous and thus only floristic homogeneity needs to be tested, or that structural and environmental heterogeneity not expressed in the floristic component is irrelevant.

Homogeneity was first discussed by Nordhagen (1923) and soon became the object of a polemic between Kylin and Romell (cf. Kylin, 1923, 1926; Romell, 1925, 1926). Kylin, assuming that, on the average, the species in a community are distributed randomly, regarded homogeneity as depending on variations in density among the species and suggested that species-area curves and frequency-distribution curves are useful tools for determining the homogeneity of a patch of vegetation. Kylin (1926) distinguished homogeneity of vegetation based on the distances between the individuals of a species, which is homogeneity in the sense of Nordhagen (1923), from homogeneity of vegetation based on distances between all the various species, which deals with the composition of the vegetation. Romell (1925, 1926), who also distinguished homogeneity of distribution from homogeneity of composition, pointed out that, with respect to the former, homogeneity is a matter of scale. Although a patch of vegetation might be heterogeneous if studied on a small scale, as a consequence of the fact that plant-individuals occur as discrete units, the same area might be homogeneous when studied on a larger scale. This matter of scale also applies to plants occurring in clumps (compare also Goodall, 1954a, 1961, 1970; Van der Maarel, 1966a). Since plant individuals are more often under- or overdispersed (cf. Ashby, 1948; Goodall, 1952, 1970; Augarde, 1957; Greig-Smith, 1964; Kershaw, 1964; Segal, 1969) than randomly distributed, the question of scale is of crucial importance in statistical tests for homogeneity. Thus, Tuomikoski's (1942) proposal to determine homogeneity on lack of correlation between the occurrence of different species is meaningless unless the question of scale is regarded at the same time.

Dahl & Hadac (1949) gave a definition of homogeneity that is often regarded as fairly satisfactory: "A plant species is said to be homogeneously distributed within a certain area if the probability of finding an individual of a plant species within a test area of given size is the same in all parts of the area. A plant community is said to be homogeneous if the individuals of the plant species which we use for the characterization of the community are homogeneously distributed". They further point out that plant communities are never fully homogeneous, and that one should be satisfied with more or less homogeneous plant communities. They also state that "the human eye, badly adapted to measurement, but well to comparison, rapidly gives the trained sociologist an impression of whether a plant community he has before his eyes is highly homogeneous or not". As pointed out by Goodall (1961), the definition by Dahl & Hadac (1949) does not fit vegetation with a mosaic pattern. Goodall (1961) then suggested the following definition: "the distribution of a species in an area of vegetation is homogeneous if there exists some sample size for which the variation between replicate samples is independent of the distance between them". Hence, the question of homogeneity is linked to the concept of minimum area. If homogeneity in the sense of Goodall (1961) could be proved, then a statistically valid minimum area would exist (cf. Goodall, 1961; Kershaw, 1964). Testing Goodall's definition involves,

however, a considerable amount of cumbersome field work and computation. Besides, this and other tests usually do no more than give an indication of the degree of heterogeneity.

Since many ecologists agree with Greig-Smith (1964), that "empirical description of vegetation cannot wait for clarification of theoretical concepts", in particular not if these concepts bear relatively little importance in many fields of ecological interest, the suggestion by Dahl & Hadac (1949) to assess homogeneity subjectively has often been accepted (e.g. Ellenberg, 1956; Dahl, 1957; Braun-Blanquet, 1964; Daubenmire, 1968; Knapp, 1971). For instance Daubenmire (1968) defines a homogeneous patch of vegetation as "one in which variations are attributable to chance, rather than to intrinsic habitat factors", and comments that one should not try to find homogeneity but rather try to eliminate as much heterogeneity as possible. This should be done subjectively, because "the results of lengthy computation often do no more than verify vegetation discontinuities that are evident to a trained synecologist by careful inspection". An ecological definition of homogeneity is given by Godron (1968): "une station est homogène lorsque chaque espèce peut y trouver des conditions de vie équivalentes d'une extrémité à l'autre, et non pas en tous les points de la station" (a stand is homogeneous when every species experiences equivalent living conditions throughout the entire extent of the stand and not necessarily in every point of it). Information theory tests to determine homogeneity have been applied by Godron (1966). Since statistical testing of homogeneity is cumbersome, many ecologists take the practical approach of subjectively assessing homogeneity of the plot in terms of the least possible obvious heterogeneity in floristics, structure and environmental features.

#### 1.4 Minimal area and plot size; plot form

Another much-discussed and criticized concept is that of minimal area, dealt with recently by Werger (1972) and Moravec (1973). Two basic approaches to the concept of minimal area can be observed:

(1) The approaches based on the community-unit theory try to determine a certain minimal size of area in which the community can be represented. The determination of this size of area is important, since communities can be sampled most efficiently with plots the size of minimal area or slightly larger. If a community is sampled with plots smaller than the minimal area then the community-type cannot easily be extracted from the data; if it is sampled with plots larger than the minimal area then much effort is wasted.

(2) One aim of the statistical approach to vegetation is to establish whether plant communities exist or not. This involves pattern studies that lead automatically to studies of minimal area, again as the minimum size of area in which the community, if it exists, can be represented.

In the community-unit theory approaches, however, the analytic and synthetic concepts of minimal area are often confused. The analytic concept of minimal area implies determination of the size of area on which a phytocoenosis (community, in Whittaker's (1956, 1962) terminology) is fully represented, in order to ascertain a suitable plot size for sampling that and similar phytocoenoses. The synthetic concept of minimal area implies determination of the average size of area on which a particular association (community-type, in Whittaker's (1956, 1962) terminology) is represented. To determine this area it is, amongst other requirements, necessary to know the

total number of species of an association (compare Raabe's remarks following a paper by Van der Maarel, 1970). Due to the varying distance between the species within each of several phytocoenoses of the same association, Raabe regarded it as impossible to determine the minimal area of an association. Only the minimal area of a particular phytocoenosis can be determined.

Since the problem of a suitable plot size for sampling vegetation is more important in vegetation survey than the possible determination of the minimal area of an association, the analytic concept of minimal area will be further considered here.

Braun-Blanquet (1913) originally determined minimal area as the area above which no new species occur in the association (probably meaning the phytocoenosis). This size of area is determined with the species-area curve (cf. Werger, 1972). Later Braun-Blanquet (1928, 1951, 1964) modified this to the area at which the species-area curve becomes more or less horizontal (cf. also Ellenberg, 1956). Recently, Tüxen (1970c) reinterpreted this curve, regarding it as consisting of three phases: (a) a strongly curved phase; (b) a slanting straight line; (c) a horizontal line. It seems that this reinterpretation deserves further investigation to establish to what degree the three phases are a result of scale and a neglect of mathematical interpolation.

Relative scales of abscissa and ordinate axes are important in determining the position of the inflection point of the species area curve (Cain & Castro, 1959; cf. Werger, 1972).

The Uppsala School defined minimal area as the area above which there was no increase in constant species, constant species being those with a percentage frequency over 90% on an area of sufficient size, that is, above the minimal area. The constancy-area curve is supposed to show a step above which only extremely large areas would add new constant species (Du Rietz *et al.*, 1920; Du Rietz, 1921).

Poore (1964, 1968) constructed species-area curves for stands of a tropical rain forest in Malaysia and found that only the curves for constant tree species flattened out. Hopkins (1955, 1957), however, could neither find a break in the species-area curves nor a step in the constancy-area curves from data of several British stands of vegetation. Goodall (1970) argued that the asymptotic form of the species-area curve is an illusion due to the use of linear scale for a measure of area.

After he had made a detailed study of Dutch dune vegetation, Van der Maarel (1966a) concluded that minimal area cannot satisfactorily be defined as an absolute intrinsic character of the vegetation and advocated a pragmatic approach, defining minimal area as the minimal size of area to be analysed to get a representative view of a phytocoenosis.

Several other definitions of minimal area were attempted (cf. Goodall, 1952; Werger, 1972) without solving the matter.

Calléja (1962), Segal (1969), Van der Maarel (1970), Werger (1972) and others emphasized that, apart from floristic richness, minimal area also depends on structure of the phytocoenosis. Thus, the species-area relation is an interwoven expression of floristic richness and structure of a patch of vegetation.

Statistical tests, usually based on homogeneity assumptions in a phytocoenosis, failed to determine a minimal area objectively (cf. Goodall, 1954b, 1961; Greig-Smith *et al.*, 1963; Greig-Smith, 1964; Kershaw, 1964), with the possible exception of some vegetation types in Western Australia (Goodall, 1963).

Werger (1972) concluded that no convincing minimal-area definition had been formulated and regarded the concept unsuitable for ascertaining a suitable plot size for sampling the vegetation. He suggested that optimal plot size be determined rather than minimal area, and described a procedure for doing so based on the regression equation of Gleason (1925) and observations by Williams (1943) that the average uniform stand or phytocoenosis seems to be manifested within an area of about a half to one hectare. Optimal plot size determined according to this procedure appeared to depend on floristic richness and structure of various phytocoenosis (cf. Werger, 1972, 1973a). This agrees with the previously mentioned arguments of Raabe (see Van der Maarel, 1970) and indicate that suitable plot size is likely to differ slightly from phytocoenosis to phytocoenosis, even if they belong to the same community.

Moravec (1973) has recently proposed using the relationships between area and similarity- and homogeneity-coefficients to determine minimal area. After taking a number of nested quadrats (more than five) in a phytocoenosis, he calculated the similarities and homogeneity-coefficients between quadrats of the same size. To calculate similarity he used Ceska's (1966) formula and to calculate homogeneity-coefficients, Moravec's (1971b) formula. Plotting the mean similarity- and homogeneity-coefficient values against increase of area, resulted in quickly rising curves which, after reaching certain values, fluctuated around these values or even decreased. He regarded as the minimal area of the phytocoenosis the area corresponding to the value reached by the curves after which they started to fluctuate or decrease. Although this seems to be a promising approach, Moravec (1973) found that it did not give unequivocal results in phytocoenoses showing a regular increase in species with regularly decreasing density.

In the Zürich-Montpellier method one is neither bound to a fixed plot size, nor to a fixed plot form in sampling the vegetation of a region, because species are rated on a cover-abundance scale with relative values. It is important that plot size be adapted to give a more or less typical description of the phytocoenosis that is represented by the vegetation in the plot, and that the vegetation in the plot should represent an example of one vegetation type only (compare Chapters 1.2 and 1.3 above).

### 1.5 Structure

In sampling, an important decision with regard to the structure of a phytocoenosis has to be taken, namely, the decision on structural homogeneity. Particularly in semi-arid, open shrubby vegetation, such as the hillside vegetation of the Karoo, low trees and shrubs are often scattered, singly or in small groups, over an open vegetation of dwarf shrubs and grasses. Under these low trees and shrubs certain smaller species occur, which are usually not found in the open dwarf-shrub layer (cf. Werger, 1973a). One can regard such a vegetation as consisting of a mosaic of two vegetation types, a dwarf shrub and grass community, and a low tree and shrub community. However, one can also regard it as consisting of one vegetation type. In this example, the latter view should be taken for the following reason. If it were a mosaic of two communities one would expect to find locally more extensive homogeneous patches of either of the two communities. This is, however, not the case. The hillside vegetation of the Karoo represents, apparently, a stable ecological-sociological equilibrium of different growth forms that constitute one inseparable entity. That certain species occur only

under the shrubs or low trees should be interpreted as a consequence of their specific ecological amplitude, and the occurrence of low trees and shrubs in the community, which have an impact on microclimate and local soil moisture conditions. Moreover, the absence of more extensive homogeneous patches of such a vegetation of low trees or shrubs with a specific understory, strongly suggests that the trees or shrubs do not constitute a vegetation type on their own, and that the hillsides of the Karoo are not covered with a close mosaic of two communities but with one open shrub community. A similar structure was recently reported by Oberdorfer (1970) from the Canary Isles, and Dahl & Hadac (1949) interpreted, according to the same principles, a superficially similar structure from South Norway, that was properly considered a mosaic of two communities.

In general, samples should be taken in such a manner that each plot adequately represents the structure of the surrounding vegetation. Thus, the plot line can often cut halfway through a small group of shrubs, rather than including either a complete group of shrubs or of the dwarf shrubs and grass vegetation only.

Another feature of structure in a phytocoenosis is stratification. Various vegetation layers can often be recognized in a phytocoenosis, sometimes clearly distinguishable from each other, at other times hardly recognizable as separate strata. In the Zürich-Montpellier School it is believed that these strata are in mutual ecological interaction and cannot be considered as separate, independent ecological units (Braun-Blanquet, 1964; Westhoff, 1967, 1968; Boerboom, 1960). There are exceptions to this rule, such as in the case of crustal lichen communities on tree trunks (cf. Barkman 1958), because such communities do not root in the same substratum as the trees and other layers, and in the case of aquatic communities (cf. Den Hartog & Segal, 1964; Segal, 1965; Westhoff, 1967; Westhoff & Den Held, 1969), although there is not unanimity in the latter case (De Lange, 1972). However, the question of scale also plays a role. In order to have a record of the structure of a sampled phytocoenosis, Zürich-Montpellier workers traditionally keep notes at each plot of the various vegetation layers distinguished, their ranges in height and an estimation of the aerial cover of each layer. An estimation of total aerial cover of the entire vegetation of the sample plot, including all strata, is also recorded.

Tüxen (1957) proposed a simple formula for comparison of the cover values of the various vegetation strata and thus the structure of vegetation samples. However, since the various layers of a phytocoenosis are not always clearly separable from one another this procedure is of only limited value.

#### 1.6 Floristic lists

At each sample site complete lists of the species occurring in the plot should be drawn up. These can include vascular plants as well as mosses, hepatics, lichens, fungi, algae, and other organisms. Since the later extraction of syntaxa in phytosociological tables is based on these floristic lists, it is of great importance that all species of the taxonomical groups considered, which are present in the plot, be recorded and that the plant individuals should be correctly identified. The requirement of complete species lists cannot easily be met in arid and semi-arid areas, since, depending on irregular rainfall, some geophytes and annuals might not be visible every year or at any particular time of the year (cf. Werger & Leistner,

1973). Complete species lists would thus require multiple visits to each plot site. The extent of a study area and the time available for study often do not allow this, so that one has to utilize permanently recognizable species in such cases (cf. Werger *et al.*, 1972; Werger, 1973 a, b). In floristically rich areas particularly this is usually not a serious drawback and the communities can be clearly characterized floristically on the bases of floristic lists in which only permanently recognizable species are entered. Furthermore, Batanouny & Abu El-Souod (1972) concluded that in arid regions perennials are generally better indicators of specific habitat factors than ephemerals. The results of the survey by Leistner & Werger (1973) of the southern Kalahari, seem to confirm this conclusion. Also Grunow (1965), Ayyad & Ammar (1973) and Zohary (1973) indicate the relatively unimportant role of annuals in vegetation classification in dry regions, but Garcia-Moya (1972) found them very useful in a phytosociological classification of arid vegetation of Arizona.

A species which occurs in more than one vegetation layer of the plot is sometimes recorded for every layer in which it occurs and each time rated on the cover-abundance and sociability scales (see below). This is especially important in, for example, rejuvenation studies in forests and in succession studies.

Some workers have included animal species in their plot lists in an attempt to delineate types of biocoenoses (see Braun-Blanquet, 1964; Tüxen, 1969). Studies that have taken smaller animals like Arthropoda or Mollusca into account, have been markedly successful (e.g. Molinier, 1960).

Although the Zürich-Montpellier system is based on floristics, this is not necessarily the only criterion for a detailed classification system of vegetation (cf. Langford & Buell, 1969). In an ordination study Knight & Loucks (1969) used structural-functional characters, such as life form, leaf size, pollination mechanism, bark thickness, seed-dispersal mechanism, etc., regardless of species, to group stands of forest. Limitations of such an approach are due to structural-functional characters usually not being unanimously acceptably defined as are species. Further, such an approach often requires a better autecological knowledge of species in the plot, than has been gained of the species of most areas.

#### 1.7 Cover-abundance

The relative importance of each species in a quadrat is assessed on the well-known cover-abundance scale used by the Zürich-Montpellier School (Braun-Blanquet, 1928, 1951; Ellenberg, 1956; Becking, 1957; Schmithüsen, 1968; Knapp, 1971). This scale, which is based partly on cover and partly on abundance, has received a good deal of criticism (Barkman *et al.*, 1964). Cover refers to aerial cover, or the area covered when the canopy is vertically projected onto the ground. Cover and abundance are estimated. Although this is basically a subjective procedure, the estimates of different phytosociologists analysing the same patch of vegetation, prove to be amazingly similar, so that the procedure is not entirely haphazard (Dahl, 1957; Van der Maarel, 1966b). The common cover-abundance scale, which is easily comparable with other cover-abundance scales such as the Domin-scale (cf. Becking, 1957), reads as follows:

- r Very rare and with a negligible cover, (usually a single individual).
- + Present but not abundant and with a small cover value (less than 1% of the quadrat area).

1 Numerous but covering less than 1% of the quadrat area, or not so abundant but covering 1–5% of the quadrat area.

2 Very numerous and covering less than 5% of the quadrat area, or covering 5–25% of the quadrat area independent of abundance.

3 Covering 25–50% of the quadrat area independent of abundance.

4 Covering 50–75% of the quadrat area independent of abundance.

5 Covering 75–100% of the quadrat area independent of abundance.

As shown, scale-units 3, 4 and 5 refer to cover, whereas the other scale-units can refer to cover and abundance. Barkman *et al.* (1964) argued that the steps in the scale are not proportional to one another and that the combination of abundance and cover in one and the same scale is in principle illogical. They criticized particularly the broad definition of scale-unit 2. Without altering the basic units of the cover-abundance scale, they advocated modifications by adding secondary symbols to the above-listed ones. This had the advantage of enabling more precise and narrower definitions of the scale-units, and floristic lists rated on their scale allowed direct comparison with older ones rated on the traditional Zürich-Montpellier scale by simply disregarding the additional symbols. The scale of Barkman *et al.* (1964) appears, however, to be more suitable for detailed survey of permanent quadrats, and the like. Only their modification of scale-unit 2 was adopted in some vegetation surveys in South Africa (Werger, 1973a, b), reading as follows:

- 2m Very numerous, covering less than 5% of the quadrat area.
- 2a Covering between 5 and 12% of the quadrat area independent of abundance.
- 2b Covering between 13 and 25% of the quadrat area independent of abundance.

A useful and practical way of estimating cover is in terms of the average canopy diameter of individuals of a species. Assuming a circular form to species, it can be readily calculated that the following relationship exists independently of the size of the particular diameter (data from the Botanical Research Institute, Pretoria):

diameters apart	cover	Z-M symbol
more than 8	less than 1%	+
8 to 3	1 to 5%	1
3 to 1	5 to 25%	2
less than 1	more than 25%	3, 4 or 5

In the latest edition of his *Pflanzensoziologie*, Braun-Blanquet (1964) slightly changed the cover-abundance scale without giving reasons for doing so. Instead of the traditionally used lower limit of 5% of scale-unit 2, he now takes 10% as the lower limit. This is very disadvantageous as the traditional scale was used for about half a century and an extensive data collection has been built up. The new definition of scale-unit 2, which does not constitute an obvious improvement, can thus only be confusing and should be avoided.

### 1.8 Sociability

All species occurring in a quadrat are often also rated on the sociability scale which is devised to indicate the grouping of individuals of the same species. For this purpose, any sprout coming out of the

soil is regarded as a separate individual, regardless of its subterranean connections with other "individuals". The scale, which is "circular" rather than linear (cf. Barkman *et al.*, 1964), reads as follows:

- 1 Single individuals.
- 2 Grouped or tufted.
- 3 In troops, small patches or cushions.
- 4 In small colonies or extensive patches, or forming carpets.
- 5 In extensive crowds or pure populations.

As clearly pointed out by Barkman (1958), it is not the sociabilities of different species that are compared, but the sociabilities of the same species in different habitats.

Many workers consider that sociability is a specific feature of each species and they regard it an unnecessary recording (e.g. Ellenberg, 1956; Barkman *et al.*, 1964), whereas others emphasize its importance and document how certain species have varying degrees of sociability under different ecological conditions and in different associations (Meltzer & Westhoff, 1942; Pfeiffer, 1962; Braun-Blanquet, 1964).

Van der Maarel (1966a, 1970) emphasized the correlation of the sociability of a species with its growth form, and used a modified sociability scale for studying vegetation structure.

If the sociability of the species in a community remains largely the same, its summarized values are often listed in the end column of the phytosociological table in order to avoid enlarging the table unnecessarily.

### 1.9 Other analytic characters of the vegetation

Many other analytic characters of the flora and vegetation in a quadrat can be recorded, such as local frequency, density, vitality, fertility, phenology, growth and life form of the species, and yield of the vegetation in the quadrat. Some of these characters are more commonly used in detailed studies of permanent quadrats, or are suitable for special purpose studies.

For vitality, a number of scales have been developed (Barkman, 1958; Braun-Blanquet, 1964; Knapp, 1971). Life forms are usually determined following the system of Raunkiaer (1934), or modified versions of it (e.g. Ellenberg, 1956; Braun-Blanquet, 1964; Ellenberg & Mueller-Dombois, 1967). For growth forms, comprehensive systems have been worked out (e.g. Schmithüsen, 1968).

### 1.10 Habitat characteristics

At each quadrat site, habitat characteristics are noted. Such notes may be rather superficial or reach a high degree of detail, and should generally be in correspondence with the purpose and scale of the survey and the time available. For instance, statistical ecologists, who are often more interested in plant-habitat correlations than merely in a multi-purpose classification system (cf. Lambert & Williams, 1962; Lambert & Dale, 1964), often aim for a rather detailed habitat characterization. The phytosociological school of Emberger in Montpellier records habitat features in great detail. Standard checksheets were developed for this purpose (Godron, 1968). The importance of standardization of habitat observations is emphasized by Godron & Poissonet (1970).

It is obvious that the more precisely habitat observations are made the more clearly associations extracted from the data can be characterized ecologically later. Apart from the usual identifying information such as locality, date of sampling and size of the plot, the following can also be important:

- (a) height above sea level;
- (b) position in the landscape;
- (c) slope angle and slope direction;
- (d) details on soil profile, soil depth, rockiness of the soil, etc.;
- (e) water table;
- (f) geological substrate;
- (g) climatic information.
- (h) biotic and other influences;

These data are often entered in the headings of phytosociological tables, together with information on vegetation layers, total cover and total number of species in each plot sample.

### 1.11 Relevé

Such a completed site record of species, their relative importance, other analytic characters of flora and vegetation, and habitat notations is generally called a relevé.

An appropriate definition of the term relevé is given by Godron (1968): "Le relevé est un ensemble d'observations écologiques et phytosociologiques qui concernent un lieu déterminé" (The relevé constitutes the total of ecological and phytosociological observations at a certain point).

### 1.12 Number of relevés

There is no fixed rule concerning the exact number of relevés needed to survey an area adequately. The number depends entirely on the scale of the survey, the variety in the survey area and the degree of precision which one wants to achieve. At the "Centre d'Etudes Phytosociologique et Ecologique" at Montpellier the number of relevés to be taken in an area is determined by the size and heterogeneity of the area and the cost of sampling (Godron, pers. comm.). Statisticians agree that a higher sampling intensity reduces the variance in the data more effectively than improved sampling precision (Goodall, 1970). The total set of relevés taken should as adequately as possible reflect the total variety in the study area. Even distribution of relevés over the study area usually ensures this. In exceptional cases, such as for example that of the dune area of the southern Kalahari (Leistner & Werger, 1973), there is so little variation in the study area, and homogeneous phytocoenoses cover such extensive areas that an even spread of the relevés is not strictly necessary.

The statement by Shimwell (1971) that the number of relevés collected is "usually less than the manageable number of 40" is meant to illustrate when a start with tabulation can be made and should not be interpreted as binding advice.

For the compilation of a sound phytosociological classification system, a large number of relevés from a wide area is necessary (cf. Tüxen, 1970b).

## 2. SYNTHESIS

The synthetic stage of the survey follows the sampling of the field data and should finally lead to interpreted results. Several concepts and technical procedures used in the process of synthesis are briefly elucidated below.

### 2.1 Tabulation

The compilation of phytosociological tables from field data has been described in great detail by Ellenberg (1956), and English and French translations of that account have been published by Küchler (1967) and Gounot (1969), respectively. Shimwell (1971) has also discussed the tabulation procedures in English so that only a brief outline need be given here.

The field data are entered into a matrix in which the rows represent species and the columns relevés. When this matrix is completed, the result is called the 'raw table'. The next step is a visual study of the association between species. Positive as well as negative association is important (Tuomikoski, 1942). The matrix is rearranged so that positively associated species are grouped together, apart from the general and the most infrequent species that do not show clear discriminant floristic associations and are listed in the lower part of the table. A species' membership of a species group is not necessarily determined by association with any individual species in that group; it can also be based on the restriction of the species to the general distribution range in the table of a group of associated species. A second rearrangement of the matrix places the relevés with a strongly similar species content together. These successive rearrangements of rows (species) and columns (relevés) in the matrix should be continued until a clear pattern of mutually discriminant nodes of species-relevé groups is obtained. This way of grouping species and relevés into species-relevé groups is in theory similar to taxonomical classification procedures in which, according to Hull (1964-65) "usually no one particular property or set of properties is necessary and any one of numerous sets is sufficient". Wittgenstein (1960) originally discussed this classification process under the term "Familienähnlichkeiten", or family resemblances (cf. Gilmour & Walters, 1964; Bambrough, 1966; Khatchadourian, 1966; Werger, 1973a).

Compilation of a final phytosociological table from a raw table may be facilitated by the use of certain expedients, such as the apparatus described by Müller *et al.* (1972). The latter authors also give a brief review of similar useful tools.

The process of rearranging a raw table into a final phytosociological table is largely objective, as has been emphasized by Ellenberg (1956) and demonstrated by Spatz & Siegmund (1973) and Coetzee & Werger (1973). The latter authors carried out hierarchical syndrome analysis on Fynbos data, which had previously been used to construct phytosociological tables. The results of the analysis matched well with the structure of the tables. Spatz & Siegmund (1973) developed a computer programme to prepare phytosociological tables. They took data from Ellenberg (1956) and were able to compile a computer-made table, which was nearly identical to that made by hand by Ellenberg. This and several other computer-based methods might yield even better results when quantitative measures of absence similar to those described by Swan (1970) are used.

It is common practice to place the individual relevés within a nodum in a specific sequence. This sequence can be according to decreasing total number of species, according to any environmental gradient observed, or to any other varying character of the vegetation or habitat observed (Braun-Blanquet, 1964). Species are usually placed in order of presence in each nodum. Table units which differ greatly from one another in floristics are often presented in separate tables.

The question of whether or not to leave unrepresentative relevés out of the final table has been discussed at great length. Both sides have convincing arguments for their points of view. Tüxen (in lit.), for instance, argues that in initial surveys the object is not so much to show all possible transitions and fragmentary forms in which an association can occur, but to describe syntaxa as clearly and definitely as possible. Heterogeneous, transitional and fragmentary relevés should thus be omitted from the table. Zonneveld (1960), Segal (1969), Gounot (1969) and Klötzli (1972), on the other hand, strongly reject the practice of leaving "bad" relevés out of the table. According to Gounot it is possible in such cases that the table is an illustration of the author's preconceived ideas rather than a means of syntaxonomical research. He adds, however, that such practices do not invalidate the method as such, but merely throw doubt upon certain results. The present author considers that, in addition, the retention of relevés that are atypical representatives of a nodum has definite advantages in initial studies of undescribed areas, since there relevés may well prove valuable data for the later recognition of previously unrecognized and undersampled syntaxa. In this context, it is worthwhile referring to Westhoff & Den Held (1969), who argue that once a proper syntaxonomical system is available, intermediate or transitional relevés are valuable in that they give information on the habitat of these transitional vegetation stands. They show that the transitional habitat is a mixture of the habitat requirements of the communities that constitute the transitional stand. The relative importance of the various habitat factors is in direct correspondence with that of the constituent communities. Therefore, relevés should not be rejected on prejudice. Each relevé should be interpreted and a relevé should, at most, be omitted from the table when it appears to be clearly heterogeneous.

## 2.2 Synthetic characters, character species, differential species

A finalized phytosociological table contains far more information than the sum of the information in each relevé (Tüxen, 1970b). It displays the main synthetic characters of a community. Since the species are arranged according to presence within the noda, the phytosociological table shows, at a glance, the constant or dominant species. A number of species will occur constantly over the entire table, whereas others will be limited, completely or largely, to one or a number of noda or table-units, that may, after ecological confirmation, represent communities. These species that are restricted in their occurrence are faithful to one or more noda or possible communities. They may be called differential species, because they differentiate between noda (cf. Ellenberg, 1956; Damman, 1964). This need not coincide with a high presence value within the nodum. Faithfulness to a community or certain communities is called fidelity and is a synthetic character. Besides presence, fidelity can also be based on cover-abundance, sociability and vitality values (Pfeiffer, 1962; Braun-Blanquet, 1964; Segal, 1969; Westhoff & Den Held, 1969). The Zürich-Montpellier School, following Szafer & Pawlowski, recognizes five degrees of fidelity—

species that are exclusive to a community in a particular geographical region, are called exclusive (*treu*);

species that are found mainly in one particular community and seldom in others, are called selective (*fest*);

species that are found optimally in one community, although they also occur in several others, are called preferential (*hold*);

species that are indifferent to a particular community, are called indifferent or vague (*vag*); and

species that are uncommon or rare in a particular community, are called strange (*fremd*).

Only exclusive, selective and preferential species are character species (Ellenberg, 1956; Becking, 1957; Braun-Blanquet, 1928, 1951, 1964; Knapp, 1971; Shimwell, 1971). Originally it was thought that most communities would contain exclusive species (cf. Braun-Blanquet, 1915). When more data became available it appeared that more species were selective or preferential rather than exclusive. Then, also, the concept of differential species was first introduced by Koch (1925). This is a species that is preferential for a certain community and, therefore, distinguishes this community from floristically related communities, but it is at the same time equally well or even better represented in still other communities. Differential species were initially used only to distinguish sub-associations and variants of associations, but gradually it became common practice to use differential species also to characterize associations and higher syntaxonomical units (Becking, 1957). Tuomikoski (1942) pointed out that character species are but a special case of differential species. With the accumulation of data from various parts of Europe it became clear that few species are faithful to a specific community over its entire distribution area. Those species that are, are called absolute character species (Braun-Blanquet, 1951; Becking, 1957; Westhoff & Den Held, 1969; Knapp, 1971; Westhoff & Van der Maarel, 1973). When the distribution area of a species exceeds that of the association in which it is found, it often occurs that the species is faithful to a specific association in one part of its distribution area and to another vicarious association in another part. Such species are called territorial or regional character species (Braun-Blanquet, 1951; Becking, 1957; Westhoff & Den Held, 1969; Westhoff & Van der Maarel, 1973). It often occurs, however, that certain species are faithful only in a limited part of the range of the association. These species are called local character species (Becking, 1957; Westhoff & Den Held, 1969; Oberdorfer, 1968; Knapp, 1971; Westhoff & Van der Maarel, 1973). Meijer Drees (1951) and Becking (1957) elucidated these geographically-based concepts of character species in clear diagrams. Becking (1957) also took the relative size of the range common to association and species into account and pointed out that a species on the fringe of its distribution area can characterize an association significantly whereas the same species may be without diagnostic value in its optimal range. This is a common phenomenon with an obvious ecological explanation. In its optimal range a species will not be strongly restricted by specific less favourable ecological conditions, while on the fringe of its distribution area, where the environment is rather unfavourable, it can survive only in a narrowly defined habitat (cf. also Klötzli, 1972).

In a later paper Becking (1961) suggested distinguishing between faithful presence, faithful sociability and faithful vitality. He tried to define these concepts quantitatively, but this did not prove to be useful.

Schwickerath (1944, 1954, 1968) has repeatedly attacked the concept of local character species and argued that from comprehensive studies covering the



entire range of the association, these species would appear to be either true character species or geographical differential species. According to Schwickerath, geographically-varying character species will still have a clear optimum over the entire range of the of the association, although this optimum may vary geographically. Geographical differential species occur only in a limited range of the association. They can either be largely restricted to a specific association, or they can be important in other associations as well.

Still another type of character species is the transgressive character species. Such a species is characteristic of a syntaxon above the association level, for example an alliance, but at the same time it is more characteristic of a specific association within that alliance than of the other associations in the alliance (Becking, 1957; Westhoff & Den Held, 1969).

Species which do not differentiate between communities are called accompanying or companion species. They can be constant as well as rare.

With the gradual broadening of the fidelity concept, it became more usual to characterize an association by differential species, and even by characteristic species combinations, although these practices are used with some restriction (Barkman, 1958; Westhoff & Den Held, 1969). Fidelity of species to associations can be determined only on the basis of phytosociological tables, using the method described by Schwickerath (1931) in less evident cases. Associations are not "determined in the field because species of known narrow amplitude are present", reducing the later determination of faithful species to a circular argument as Poore (1955, 1956) suggested. As pointed out by Barkman (1958), Moore (1962) and Gounot (1969), this suggestion was based on a poor understanding of the Zürich-Montpellier approach and is entirely invalid.

The East German School of Scamoni and Passarge has diverged slightly from the theory of the Zürich-Montpellier School, and uses the concept of sociological species groups. These are formed of species in the same vegetation layer, which show a similar sociological behaviour owing to similar ecological requirements. The species in one sociological group often possess similar growth-forms. In certain communities they have their maximum or optimum together, whereas they are simultaneously absent from other communities (Passarge & Hofmann, 1964, 1968; Scamoni *et al.*, 1965; Passarge, 1968, cf. Doing, 1962, 1969; Janssen, 1967; Klötzli, 1972). The theoretical and practical value of this approach has still to be shown (cf. Hohenester, 1970).

The average number of species in the relevés of a community and the community structure can also be regarded as synthetic characters of the vegetation. These topics will be dealt with in sections 2.6 and 2.7.

### 2.3 Ecological confirmation of the table pattern

The arrangement of species and relevés in the phytosociological table is not an end in itself, but should lead to a comprehensive classification system of syntaxa, that can serve as the basis for further ecological studies (Braun-Blanquet, 1964; Ivimey-Cook & Proctor, 1966; Tüxen, 1970b). When the nodes in the phytosociological table are established, their biological reality should be confirmed by demonstrating coincidence between the community-types they possibly represent and specific habitat conditions. The checking of the ecological meaning of a supposed community can be done in the field, or from the

habitat characterization of the relevés on the field sheets. Should this latter approach be used, final checking in the field is still necessary.

Confirmation of coincidence between the pattern on the phytosociological table and specific habitat conditions is necessary for the following reason:

All taxa have their ecological amplitude (which, for the purpose of this discussion, includes the effect of competition) within which they can survive and outside which they cannot exist. Species that have a high presence over the entire phytosociological table presumably have an ecological amplitude that is at least so wide as to include all habitats of the relevés making up the table. Character and differential species, however, have a smaller ecological amplitude, at least in the area where the relevés were taken. Their ecological amplitude is such that these species are unable to exist in some of the habitats of the relevés comprising the table. Because the central concept of all approaches based on the community-unit theory implies that vegetation consists of basic natural entities which are generally in contact with one another along narrow boundaries, it is supposed that more or less coincident ecological amplitudes of some species, at least to the one side, result in such a narrow boundary. Hence, if the coincidence of certain habitat conditions and a nodum section in the table can be confirmed, a basic vegetation unit, a community is delineated. Species, as indicators of a certain habitat and typical of a community, are thus indicators for the habitat typical for a community. This is also expressed by Von Glahn (1968) when he says that the vegetation type is "das maximale korrelative Konzentrat wiederholt vorkommender Artverbindungen und bestimmter Merkmalskombinationen seines Standortes". In this way it can be shown that the pattern in the table is not an artificial one due to a clever manipulation of the matrix rows and columns, but represents real, floristically- and environmentally-characterized natural entities. In the Zürich-Montpellier approach it is thus empirically determined that patterns in floristic composition correspond with patterns in the environment (cf. Goodall, 1953; Gounot, 1961, 1969; Moore, 1962; Segal, 1969; Garcia-Moya, 1972).

### 2.4 The association and other syntaxa; the constancy table

The definition, proposed by Schröter and Flahault and accepted by the Third International Botanical Congress in Bruxelles in 1910, of the basic natural community of the Zürich-Montpellier system, the association, says that it is a plant community that has a definite floristic composition, a uniform physiognomy and is bound to uniform habitat conditions. Although special weight was and is given to character species, and later to differential species, the association is not based solely on these species, but on its total floristic composition (Braun-Blanquet, 1915, 1959, 1964; Westhoff & Den Held, 1969).

Associations are subdivided into subassociations, variants and facies. Subassociations and variants are characterized by their own differential species and mostly it is only in subordinate features that their specific habitats differ from the habitat of other subassociations in the same association. A facies is characterized by the strong dominance of a specific species and possesses no character or differential species of its own (Ellenberg, 1956; Braun-Blanquet, 1964).

Associations are combined into alliances, alliances into orders and orders into classes. Alliances and orders have their own character and differential spe-

cies; classes are distinguished on the basis of character species only (Braun-Blanquet, 1964). A useful tool in the procedure of hierarchization is the so-called Roman or constancy table (although based on presence). The presence of each species within each community is rated on a five-point scale and the range of its cover-abundance value is noted:

- I Species present in 1–20% of the relevés of a community.
- II Species present in 21–40% of the relevés of a community.
- III Species present in 41–60% of the relevés of a community.
- IV Species present in 61–80% of the relevés of a community.
- V Species present in 81–100% of the relevés of a community.

Each community is thus reduced to a single column in the Roman table, so that it is easy to assess which species are faithful to the various communities.

With the development of the concepts of character and differential species, the concept of the association was also somewhat modified. Whereas, according to certain authors, the association should still possess character species (Schwickerath 1954, 1968; Braun-Blanquet, 1964; Oberdorfer, 1968) others recognize, in exceptional cases, associations that have only differential species or only a characteristic species combination (Doing Kraft, 1956; Maas, 1959; Barkman, 1958; Damman, 1964; Westhoff & Den Held, 1969; Werger, 1973a). Many association character species are only local or regional character species. According to Oberdorfer (1968), every association is therefore at the same time a regional or geographical association (Gebietsassoziation). If, in different areas of the regional association, differences occur in the species combinations of accompanying or also order and class character species, while the floristic composition of the group of association and alliance character species remains unaltered, one should distinguish geographical races of the association. If, however, the floristic composition of the group of alliance and association character species alters, different geographical associations should be distinguished (Oberdorfer, 1968). Borhidi (1963) suggested the combination of regional associations into synassociations, which would rank between regional associations and suballiances. Schwickerath (1954, 1968) wanted to recognize only geographic subassociations of an association and, as pointed out above, argues that most species, which are called local character species at present, will finally prove to be geographical differential species, whereas a few others will prove to be true character species. Knapp (1971) accepted the idea of geographical associations and suggested the combination of them into chief associations (Hauptassoziationen) or association groups (Assoziationsgruppe). As pointed out by Westhoff & Den Held (1969), several authors have recently regarded geographical associations as the real associations and promoted the chief association simply to alliance. This is one of the practices which can lead directly to what Pignatti (1968) called "the inflation of higher syntaxonomical units".

## 2.5 Nomenclature

No internationally accepted nomenclatural code for syntaxonomical use exists as yet, although, particularly since the early fifties (cf. Moravec, 1969), several attempts have been made to achieve this aim. Westhoff & Den Held (1969) point out that one of the main

reasons for the persistent failure to reach an international agreement is that the type-method as used in taxonomy, and advocated for syntaxonomical use by Barkman (1958) and Moravec (1968), is not suitable, in that it is hardly possible to designate generally acceptable type-relevés. Another difficulty results from a taxon name being intended as a label without diagnostic function, whereas the name of a syntaxon refers to one or more species occurring in it. Although a strict priority rule is often difficult to apply, priority is generally recognized as far as possible. Tentative rules were published by Meijer Drees (1954) and were commented upon by several workers in the same issue of *Vegetatio*. More recently Moravec (1968) published a renewed design for a nomenclatural code, which comprised several of Meijer Drees' proposals. The suggestions of Moravec (compare also Moravec, 1969, 1971a), which seem to have received considerable approval, deal with:

- (a) conditions for the effective and valid publication of a name;
- (b) sufficiency of the added diagnosis;
- (c) typification of the name;
- (d) priority;
- (e) retention, rejection and alteration of names;
- (f) citation of authors' names.

In the Zürich-Montpellier School syntaxa are traditionally named after one or two taxa, adding an appropriate suffix to indicate the rank of the syntaxon concerned, to the name of the genus (Braun-Blanquet, 1928, 1951, 1964). These suffixes are -etosum, -etum, -ion, -etalia and -etea for subassociations, associations, alliances, orders and classes respectively. If desirable, the specific epithet can be added in genitive form. Detailed linguistic guides for the correct formation of syntaxonomical names have been published by Bach *et al.* (1962) and in particular by Rauschert (1963).

Originally it was suggested that only character species be used for naming the associations, but this proved untenable (cf. Moravec, 1969). The only requirement that can be made at present is that the name-giving taxon must at least be present in the syntaxon concerned. It is common practice, however, that syntaxa are named after one or two of the taxa listed in the group of character and differential species. Sometimes a prominent or constantly abundant species is used in combination with a species of the character and differential species group to designate a syntaxon. The terms "inops" and "typicum" for subassociations should be used following Westhoff & Den Held (1969).

## 2.6 Homotoneity; affinities between syntaxa

As stated above, the average number of species in the relevés of a community can be regarded as a synthetic character of the community (Raabe, 1952). Comparison of such figures for various communities indicates the relative floristic richness of a community. The value for the average number of species in the relevés of a community is based on the total number of species in each relevé and is, therefore, a standard for judging the relative floristic agreement between the relevés and the communities to which they belong. When the total number of species in each relevé is more or less similar for all relevés within one community, this is an indication that the community-table is more or less homogeneous. Table homogeneity is called homotoneity in recent literature (Dahl, 1957; cf. Westhoff & Van der Maarel, 1973). Hence, the absolute value of these figures is, as far as homotoneity is concerned, theoretically unimportant.

Only the deviation of the value for each relevé from the average is important, in that it indicates to what extent each relevé is floristically representative of the entire community (Knapp, 1971). A complicating factor concerning the matter of average number of species is, of course, the number of species that are common to all relevés in a community or to only a limited number of relevés, or that are present in only one relevé in a community (cf. Tüxen, 1970c). At present there is no agreement on the theoretical implications of the homotoneity of a community-table [see, for example, the discussion following Tüxen's (1970c) exposé], but a number of procedures have been suggested to determine homotoneity. Jaccard's community coefficient is probably the oldest way of determining the similarity between two stands or relevés (cf. Ellenberg, 1956; Dahl, 1957; Becking, 1957; Barkman, 1958; Braun-Blanquet, 1964; Ceska, 1966). Jaccard's coefficient takes the form  $c/(a+b+c)$ , where relevé A is compared with relevé B, and a is the number of species occurring only in A, b the number of species occurring only in B, and c the number of species common to A and B. Poore (1955c) proposed a modification of this formula  $200c/(a+b+2c)$ . Other often-used coefficients are those of Kulczinsky and of Sørensen (cf. Dahl, 1957; Becking, 1957; Braun-Blanquet, 1964; Ceska, 1966). Kulczinsky's coefficient is similar to the one given by Poore (1955c), except that a, b, and c are presence degrees (cf. Barkman, 1958). Also, Sørensen's coefficient is similar to the others:  $2c/(a+b+2c)$ , in which a, b and c are again numbers of species (cf. Dahl, 1957; Becking, 1957; Braun-Blanquet, 1964). Ellenberg (1956) proposed the formula  $c/(2a+2b+c)$ , where a, b and c represent total cover values calculated according to Tüxen & Ellenberg (1937). Pfeiffer (1957) suggested using only the most constant species of a syntaxon, as defined by Raabe (1952) (see below), in homotoneity calculations. The homotoneity value of a syntaxon equals, according to the Pfeiffer's formula,  $100(V_1 + V_2 + \dots + V_z)/n.g$ , where  $V_1, V_2, \dots, V_z$  are the number of species in each individual relevé, n is the total number of relevés, and g the total number of species in the syntaxon. Barkman (1958) modified Jaccard's coefficient to  $c/\sqrt{ab}$  (in which a, b and c are again numbers of species). Recently, Moravec (1971b) proposed a procedure to determine the homotoneity of a set of relevés based on species with a constancy of over 60 per cent in the species composition of an "average" relevé, corrected by a factor which is proportional to the difference in species number between the richest and poorest relevé. Slightly more complicated ways of determining homotoneity were proposed by Looman & Campbell (1960) and Dahl (1960). Looman & Campbell (1960) used Sørensen's coefficient, but determined statistically the minimum value for which two relevés can still be regarded similar. Dahl (1960) proposed an index of uniformity defined as the ratio between the mean number of species per relevé and the index of diversity. Gounot & Calléja (1962) and Ceska (1966) studied the various possibilities of using Sørensen's coefficient and the latter author suggested a formula derived from it to calculate the mean floristic similarity within a set of relevés. Yet another way of determining the homotoneity of a community table is the graphical representation of the number of species in the various presence classes, based on the Roman table. If the diagram of the five presence classes is U-shaped, which means that presence classes I and V are more frequent than the adjacent in-between ones, the community is considered to be homogeneous (Matuszkiewicz, 1948; Dahl &

Hadac, 1949; Becking, 1957; Dahl, 1957; Gounot, 1961, 1969; Goodall, 1970; Björnstad, 1971; cf. Etter, 1948).

Similarity coefficients of the types discussed above, or derived ones, are also used in computer-based programs for the compilation of phytosociological tables (e.g. Spatz & Siegmund, 1973). Other computer-based programs use entirely different distance coefficients, however (e.g. Schmid & Kuhn, 1970).

Many of the above-mentioned coefficients for calculating similarity between two relevés are also used to calculate the affinities between two syntaxa (cf. Barkman, 1958; Braun-Blanquet, 1964). Here again, values for total numbers of species, total cover values (Tüxen & Ellenberg, 1937), or "Gruppenabundanz" values (Schwickerath, 1931) can be used. Raabe (1952) suggested that only the most constant species be used in the calculations. The group of most constant species would comprise the "characteristic species combination" and its number would be as large as the average number of species of the syntaxon. Barkman (1958) suggested a more complicated method based on total cover values.

## 2.7 Community structure

The definition of the association as accepted at Bruxelles in 1910 (see previous), and also more modern versions, imply, amongst other requirements, that the association should be of a uniform physiognomy. If one uses a fairly rigid physiognomic classification system such as that of Fosberg (1967), however, this requirement can often not be met (cf. Werger, 1973a, b). Owing to the rigidity of the physiognomic classification system, communities with a considerable similarity in structure can fall into completely different formation classes.

A second reason for structural heterogeneity within some associations and other syntaxa, is that due to environmental circumstances some phytocoenoses possess an additional vegetation layer as compared with other floristically similar phytocoenoses (cf. Van Donselaar, 1965; Werger, 1973a). This is a feature that is apparently related to the phenomenon of twin formations as discussed by Westhoff (1967, 1968), who adopted the term from nineteenth century publications by Hult and by Katz. Westhoff (1967, 1968) elaborates on a number of examples where structurally different variants, sub-associations or associations are combined into the same higher syntaxon because their floristic composition is strongly related. According to the floristic principle of the Zürich-Montpellier School these syntaxa cannot be equally well classified in other, structurally more similar syntaxa. Westhoff (1967, 1968) observed that these twin formations occur only where extreme habitat factors predominate. Such extreme habitat factors are usually abiotic, for example, extreme temperatures, frequent burning and a strongly-fluctuating water table, and are to such an extent overriding that vegetation structure in these places is of relatively low ecological importance. Structure should thus not be over-estimated as a diagnostic criterion in such situations and floristic criteria should normally prevail (Westhoff, 1967, 1968).

In South Africa, where mismanagement of the natural vegetation has occurred on a large scale, overgrazing and severe trampling can also be regarded as extreme habitat factors (cf. Werger, 1973a). In such cases it is clear that the floristic principle should prevail and that differences in structure should be regarded as of secondary importance in compiling a classification of vegetation.

## ACKNOWLEDGEMENTS

The following persons kindly made critical comments on the manuscript: Mr B. J. Coetzee, Dr D. Edwards, Mr J. W. Morris and Prof. Dr V. Westhoff. Their assistance is gratefully acknowledged.

## OPSOMMING

Omdat die Zürich-Montpellier metode by die bestudering van plantegroei in Suid-Afrika in die toekoms waarskynlik baie meer gebruik gaan word, word hier 'n kort beskrywing van die begrippe en tegnieke, waarvan by hierdie metode gebruik gemaak word, gegee.

## REFERENCES

- ACOCKS, J. P. H., 1953. Veld Types of South Africa. *Mem. Bot. Surv. S. Afr.* 28: 1-192.
- ADAMSON, R. S., 1938. *The Vegetation of South Africa*. London: British Empire Vegetation Committee.
- ASHBY, E., 1948. Statistical ecology. II. A reassessment. *Bot. Rev.* 14: 222-234.
- AUGARDE, J., 1957. Contribution à l'étude des problèmes de l'homogénéité en son application à la phytosociologie. *Bull. Serv. Carte Phytogéogr., Sér. B* 2: 11-23.
- AYYAD, M. A. & AMMAR, M. Y., 1973. Relationships between local physiographic variations and the distribution of common Mediterranean desert species. *Vegetatio* 27: 163-176.
- BACH, R., KUOCH, R. & MOOR, M., 1962. Die Nomenklatur der Pflanzengesellschaften. *Mitt. Flor.-Soz. Arbeitsgem. N. F.* 9: 301-308.
- BAMBROUGH, R., 1966. Universals and family resemblances. in PITCHER, G. (ed.): *Wittgenstein*. pp. 186-204. London: MacMillan.
- BARKMAN, J. J., 1958. *Phytosociology and ecology of cryptogamic epiphytes*. Assen: Van Gorcum.
- BARKMAN, J. J., DOING, H. & SEGAL, S., 1964. Kritische Bemerkungen und Vorschläge zur quantitativen Vegetationsanalyse. *Acta Bot. Neerl.* 13: 394-419.
- BATANOUNY, K. H. & ABU EL-SOUOD, S., 1972. Ecological and phytosociological study of a sector in the Lybian desert. *Vegetatio* 25: 335-356.
- BAYER, A. W., 1955. The ecology of grasslands. in MEREDITH, D. (ed.): *The grasses and pastures of South Africa*. pp. 539-550. Parow: Central News Agency.
- BECKING, R. W., 1957. The Zürich-Montpellier School of phytosociology. *Bot. Rev.* 23: 411-488.
- BECKING, R. W., 1961. Quantitative evaluation of phytosociological data. *Rec. Adv. Bot.* ? : 1346-1350.
- BEWS, J. W., 1918. *The grasses and grasslands of South Africa*. Pietermaritzburg: Davis.
- BJÖRNSTAD, A., 1971. A phytosociological investigation of the deciduous forest types in Søgne, Vest-Agder, South Norway. *Norw. J. Bot.* 18: 191-214.
- BOERBOOM, J. H. A., 1960. De plantengemeenschappen van de Wassenaarse duinen. *Meded. Landbouwhogeschool Wageningen* 60 (10): 1-135.
- BORHIDI, A., 1963. Die Zönologie des Verbandes Fagion illyricum. I. Allgemeiner Teil. *Acta Bot. Acad. Sc. Hung.* 9: 259-298.
- BRAUN-BLANQUET, J., 1913. Die Vegetationsverhältnisse der Schneestufe in den Rätisch-Lepontischen Alpen. *N. Denkschr. Schweiz. Naturf. Ges.* 48: 1-347.
- BRAUN-BLANQUET, J., 1915. *Les Cévennes méridionales (Massif de l'Aigoual)*. Genève: Soc. Gen. Impr.
- BRAUN-BLANQUET, J., 1928. *Pflanzensoziologie*. Wien: Springer. 1. Aufl.
- BRAUN-BLANQUET, J., 1932. *Plant sociology*. (transl. G. D. FULLER & H. S. CONARD). New York: McGraw Hill.
- BRAUN-BLANQUET, J., 1951. *Pflanzensoziologie*. Wien: Springer. 2. Aufl.
- BRAUN-BLANQUET, J., 1959. Grundfragen und Aufgaben der Pflanzensoziologie in TURRILL, W. B. (ed.): *Vistas in Botany* pp. 145-171. London: Pergamon Press.
- BRAUN-BLANQUET, J., 1964. *Pflanzensoziologie*. Wien: Springer. 3. Aufl.
- BRAUN-BLANQUET, J., 1968. L'école phytosociologique Zürich-Montpelliéraine et la S.I.G.M.A. *Vegetatio* 16: 1-78.
- BRAY, J. R. & CURTIS, J. T., 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27: 325-349.
- CAIN, S. A. & DE OLIVEIRA CASTRO, G. M., 1959. *Manual of vegetation analysis*. New York: Harper.
- CALLÉJA, M., 1962. Étude de la courbe aire-espèce et l'aire minimale. *Bull. Serv. Carte Phytogéogr., Sér. B* 7: 161-179.
- CESKA, A., 1966. Estimation of the mean floristic similarity between and within sets of vegetational relevés. *Folia Geobot. Phytotaxon.* 1: 93-100.
- COETZEE, B. J., 1977. 'n Plantsosiologiese studie van die Jack Scott-Natuurreservaat. M.Sc. thesis, Pretoria: Univ. Pretoria (Unpubl.)
- COETZEE, B. J., 1974. A phytosociological classification of the vegetation of the Jack Scott Nature Reserve. *Bothalia* 11(3): 329-347.
- COETZEE, B. J. & WERGER, M. J. A., 1973. On hierarchical syndrome analysis and the Zürich-Montpellier table method. *Bothalia* 11: 159-164.
- CURTIS, J. T., 1959. *The vegetation of Wisconsin. An ordination of plant communities*. Madison: Univ. Press.
- DAHL, E., 1957. Rondane. Mountain vegetation in South Norway and its relation to the environment. *Skr. Norske Vid.-Akad. i Oslo. I. Mat.-Naturv. Kl.* 1956(3): 1-374.
- DAHL, E., 1960. Some measures of uniformity in vegetation analysis. *Ecology* 41: 805-808.
- DAHL, E. & HADAC, E., 1949. Homogeneity of plant communities. *Stud. Bot. Czechoslov.* 10: 159-176.
- DAMMAN, A. W. H., 1964. Some forest types of central Newfoundland and their relation to environmental factors. *Forest Science Monogr.* 8: 1-62.
- DAUBENMIRE, R., 1968. *Plant communities. A textbook of plant synecology*. New York: Harper & Row.
- DE LANGE, L., 1972. *An ecological study of ditch vegetation in the Netherlands*. Ph. D.thesis. Univ. Amsterdam.
- DEN HARTOG, C. & SEGAL, S., 1964. A new classification of the waterplant communities. *Acta Bot. Neerl.* 13: 367-393.
- DOING, H., 1956. Het associatiebegrip en de systematiek van plantengemeenschappen volgens de methode van Braun-Blanquet. *Vakbl. v. Biol.* 36 (11): 1-13.
- DOING, H., 1962. Systematische Ordnung und floristische Zusammensetzung niederländischer Wald- und Gebüschgesellschaften. *Wentia* 8: 1-85.
- DOING, H., 1969. Sociological species groups. *Acta Bot. Neerl.* 18: 398-400.
- DOING, H., 1970. The use of phytosociological methods in various parts of the world. *Belmontia* 4 (12): 53-61.
- DU RIETZ, G. E., 1921. *Zur methodologischen Grundlage der modernen Pflanzensoziologie*. Wien: Holzhausen.
- DU RIETZ, G. E., FRIES, T. C. E., OSVALD, H. & TENGWALL, T. A., 1920. Gesetze der Konstitution natürlicher Pflanzengesellschaften. *Vetensk. Prakt. Unders. Lappl. Flora och Fauna* 7: 1-47.
- EDWARDS, D., 1967. A plant ecological survey of the Tugela River Basin, Natal. *Mem. Bot. Surv. S. Afr.* 36: 1-285.
- ELLENBERG, H., 1956. Aufgaben und Methoden der Vegetationskunde. in WALTER, H.: *Einführung in die Phytologie*. IV, 1. Stuttgart: Ulmer.
- ELLENBERG, H. & MUELLER-DOMBOIS, D., 1967. A key to Raunkiaer plant life forms with revised subdivisions. *Ber. Geobot. Inst. ETH, Stiftung Rübel* 37: 56-73.
- ETTER, H., 1948. De l'analyse statistique des tableaux de végétation. *Vegetatio* 1: 147-154.
- FOSBERG, F. R., 1967. A classification of vegetation for general purposes. in PETERKEN, G. F. (ed.): *Guide to the checksheet of conservation areas*. IBP Handbook 4: 73-120.
- GARCIA-MOYA, E., 1972. *A preliminary vegetation classification of the Tombstone, Arizona, vicinity*. Ann Arbor: Univ. Microfilms.
- GILMOUR, J. S. L. & WALTERS, S. M., 1964. Philosophy and classification. in TURRILL, W. B. (ed.): *Vistas in Botany* 4: 1-22. Oxford: Pergamon.
- GLEASON, H. A., 1925. Species and area. *Ecology* 6: 66-74.
- GODRON, M., 1966. Application de la théorie de l'information à l'étude de l'homogénéité et de la structure de la végétation. *Oecol. Plant.* 1: 187-197.
- GODRON, M., (ed.), 1968. *Code pour le relevé méthodique de la végétation et du milieu. Principes et transcription sur cartes perforées*. Paris: Centre Nat. Rech. Scient.

- GODRON, M. & POISSONET, J., 1970. Standardization and treatment of ecological observations. in FRANKEL, O. H. & BENNETT, E.: Genetic resources in plants—their exploration and conservation. *IBP Handbook* 11: 189–204.
- GOODALL, D. W., 1952. Quantitative aspects of plant distribution. *Biol. Rev.* 27: 194–245.
- GOODALL, D. W., 1953. Objective methods for the classification of vegetation. I. The use of positive interspecific correlation. *Aust. J. Bot.* 1: 39–63.
- GOODALL, D. W., 1954a. Vegetational classification and vegetational continua. in JANCHEN, (ed.): Festschrift für Erwin Aichinger. I. *Angewandte Pflanzensoziologie*. pp. 168–182. Wien: Springer.
- GOODALL, D. W., 1954b. Minimal area: a new approach. *VIII Congr. Int. Bot. Paris 1954, Sect. 7. Rapp. et Comm.* pp. 19–21.
- GOODALL, D. W., 1961. Objective methods for the classification of vegetation. IV. Pattern and minimal area. *Austr. J. Bot.* 9: 162–196.
- GOODALL, D. W., 1963. Pattern analysis and minimal area—some further comments. *J. Ecol.* 51: 705–710.
- GOODALL, D. W., 1970. Statistical plant ecology. *Ann. Rev. Ecol. Syst.* 1: 99–124.
- GOUNOT, M., 1961. Les méthodes d'inventaire de la végétation. *Bull. Serv. Carte Phytogéogr., Sér. B.* 6: 7–93.
- GOUNOT, M., 1969. *Méthodes d'étude quantitative de la végétation*. Paris: Masson.
- GOUNOT, M. & CALLÉJA, M., 1962. Coefficient de communauté homogénéité et aire minimale. *Bull. Serv. Carte Phytogéogr. Sér. B.* 7: 181–200.
- GREIG-SMITH, P., 1964. *Quantitative plant ecology*. London: Butterworth. 2nd ed.
- GREIG-SMITH, P., KERSHAW, K. A. & ANDERSON, D. J., 1963. The analysis of pattern in vegetation: a comment on a paper by D. W. Goodall. *J. Ecol.* 51: 223–229.
- GRUNOW, J. O., 1965. *Objective classification of plant communities: a synecological study in the sour-mixed bushveld of Transvaal*. D.Sc. (Agric.) thesis. Pretoria: Univ. Pretoria. (Unpubl.)
- GRUNOW, J. O. & LANCE, G. N., 1969. Classification of savanna by information analysis. *S. Afr. J. Sci.* 65: 341–348.
- GRUNOW, J. O. & MORRIS, J. W., 1969. Preliminary assessment of ecological status of plant species in three South African Veld Types. *J. S. Afr. Bot.* 35: 1–12.
- HOHENESTER, A., 1970. Idiotaxonomie und syntaxonomie. *Ber. Dtsch. Bot. Ges.* 83: 641–646.
- HOPKINS, B., 1955. The species-area relations of plant communities. *J. Ecol.* 43: 409–426.
- HOPKINS, B., 1957. The concept of minimal area. *J. Ecol.* 45: 441–449.
- HULL, D. L., 1964–65. The effect of essentialism on taxonomy—two thousand years of stasis. I. *Brit. J. Phil. Sci.* 15: 314–326. II. *Brit. J. Phil. Sci.* 6: 1–18.
- IVIMEY-COOK, R. B. & PROCTOR, M. C. F., 1966. The application of association-analysis to phytosociology. *J. Ecol.* 54: 179–192.
- JANSSEN, C. R., 1967. A floristic study of forests and bog vegetation, Northwestern Minnesota. *Ecology* 48: 751–765.
- KERSHAW, K. A., 1964. *Quantitative and dynamic ecology*. London: Arnold.
- KHATCHADOURIAN, H., 1966. Common names and “family resemblances”. in PITCHER, G. (ed.): *Wittgenstein*. pp. 205–230. London: MacMillan.
- KILLICK, D. J. B., 1963. An account of the plant ecology of the Cathedral Peak area of the Natal Drakensberg. *Mem. Bot. Surv. S. Afr.* 34: 1–178.
- KILLICK, D. J. B., 1967. Fifty years of plant ecology in South Africa. *J. S. Afr. Biol. Soc.* 7–8: 11–28.
- KLÖTZLI, F., 1972. Grundsätzliches zur Systematik von Pflanzengesellschaften. *Ber. Geobot. Inst. ETH, Stift. Rübel* 41: 35–47.
- KOCH, W., 1925. Die Vegetationseinheiten der Linthebene unter Berücksichtigung der Verhältnisse in der Nordostschweiz. Systematisch-kritische Studie. *Jb. St. Gall. Naturw. Ges.* 61: 1–146.
- KNAPP, R., 1971. *Einführung in die Pflanzensoziologie*. Stuttgart: Ulmer. 3. Aufl.
- KNIGHT, D. H. & LOUCKS, O. L., 1969. A quantitative analysis of Wisconsin forest vegetation on the basis of plant function and gross morphology. *Ecology* 50: 219–234.
- KÜCHLER, A. W., 1967. *Vegetation mapping*. New York: Ronald Press.
- KYLIN, H., 1923. Växtsociologiska randanmärkingar. *Bot. Notiser* 1923: 161–234.
- KYLIN, H., 1926. Über Begriffsbildung und Statistik in der Pflanzensoziologie. *Bot. Notiser* 1926: 81–180.
- LAMBERT, J. M. & DALE, M. B., 1964. The use of statistics in phytosociology. *Adv. Ecol. Res.* 2: 59–99.
- LAMBERT, J. M. & WILLIAMS, W. T., 1962. Multivariate methods in plant ecology. IV. Nodal analysis. *J. Ecol.* 50: 775–802.
- LANGFORD, A. N. & BUELL, F. M., 1969. Integration, identity and stability in the plant association. *Adv. Ecol. Res.* 6: 83–135.
- LEISTNER, O. A. & WERGER, M. J. A., 1973. Southern Kalahari phytosociology. *Vegetatio* 28: 353–399.
- LOOMAN, J. & CAMPBELL, J. B., 1960. Adaptation of Sørensen's K (1948) for estimating unit affinities in prairie vegetation. *Ecology* 41: 409–416.
- LOUW, A. J., 1970. *'n Ekologiese studie van Mopanie-veld noord van Soutpansberg*. D.Sc. (Agric.) thesis. Pretoria: Univ. Pretoria (Unpubl.).
- MAAS, F. M., 1959. Bronnen, bronbeken en bronbossen in Nederland, in het bijzonder van de Veluwezoom. *Meded. Landbouwhogeschool Wageningen* 59 (12): 1–166.
- MARLOTH, R., 1908. Das Kapland, insonderheit das Reich der Kapflora, das Waldgebiet und die Karroo, pflanzengeographisch dargestellt. *Wiss. Ergebn. Dtsch. Tiefsee-Exped. "Waldivia" 1898–1899*. II, 3. Jena: Fischer.
- MATUSZKIEWICZ, W., 1948. Róslinnosc lasów okolic Lwowa (The vegetation of the forests of the environments of Lvov). *Ann. Univ. Mariae Curie-Skłodowska, Sect. C.* 3: 120–193. (engl. summ.).
- MEIJER DREES, E., 1951. Enkele hoofdstukken uit de moderne plantensociologie en een ontwerp voor nomenclatuurregels voor plantengesellschaften. *Rep. For. Res. Inst. Bogor, Indonesia* 51: 1–218.
- MEIJER DREES, E., 1954. A tentative design for rules of phytosociological nomenclature. *Vegetatio* 4: 205–214.
- MELTZER, J. & WESTHOFF, V., 1942. *Inleiding tot de plantensociologie*. 's Graveland: Breughel.
- MOLINIER, R., 1960. Etude des biocoenoses du Cap Corse. I. *Vegetatio* 9: 121–192. II. *Vegetatio* 9: 217–312.
- MOLL, E. J., 1969. An investigation of the plant ecology of the Havaan forest, Natal, using an ordination technique. *Bothalia* 10: 121–128.
- MOORE, J. J., 1962. The Braun-Blanquet system: a reassessment. *J. Ecol.* 50: 761–769.
- MOORE, J. J., FITZSIMONS, P., LAMBE, E. & WHITE, J., 1970. A comparison and evaluation of some phytosociological techniques. *Vegetatio* 20: 1–20.
- MORAVEC, J., 1968. Zu den Problemen der pflanzensoziologischen Nomenklatur. in Tüxen, R. (ed.): *Pflanzensoziologische Systematik*. *Ber. Int. Symp. Stolzenau* 1964. pp. 142–154. Den Haag: Junk.
- MORAVEC, J., 1969. Die Vorbedingungen der pflanzensoziologischen Nomenklaturregeln. *Acta Bot. Croatica* 28: 259–265.
- MORAVEC, J., 1971a. Bericht über die Tätigkeit der Nomenklaturkommission der Internationalen Vereinigung für Vegetationskunde 1969–1970. *Vegetatio* 22: 251–254.
- MORAVEC, J., 1971 b. A simple method for estimating homogeneity of sets of phytosociological relevés, *Folio Geobot. Phytotaxon.* 6: 147–170.
- MORAVEC, J., 1973. The determination of the minimal-area of phytocoenoses. *Folia Geobot. Phytotaxon.* 8: 23–47.
- MORRIS, J. W., 1969. An ordination of the vegetation of Ntshongweni, Natal. *Bothalia* 10: 89–120.
- MÜLLER, P. J., WERGER, M. J. A., COETZEE, B. J., EDWARDS, D. & JARMAN, N. G., 1972. An apparatus for facilitating the manual tabulation of phytosociological data. *Bothalia* 10: 579–581.
- MYRE, M., 1960. Alguns tipos de graminais do sul da provincia de Moçambique. *Anais Serv. Agric. Flor. Moç.* 1960.
- MYRE, M., 1962. A grassland type of the south of the Moçambique province. *C. R. IV. Reun. AETFAT*. pp. 337–362.
- MYRE, M., 1964. A vegetação do extremo sul da provincia de Moçambique. *Junta Inv. Ultramar, Est., Ens. e Doc.* 110: 1–145.
- NORDHAGEN, R., 1923. Om homogenitet, konstans og minimum areal. Bidrag til den plantesociologiske diskussion. *Nyt. Mag. f. Naturvid.* 61: 1–51.

- OBERDORFER, E., 1968. Assoziation, Gebietsassoziation, geographische Rasse. in TÜXEN, R. (ed.): Pflanzensozilogische Systematik. *Ber. int. Symp. Stolzenau* 1964. pp. 124-141. Den Haag: Junk.
- OBERDORFER, E., 1970. Pflanzensozilogische Strukturprobleme am Beispiel kanarischer Pflanzengesellschaften. in TÜXEN, R. (ed.): Gesellschaftsmorphologie. *Ber. Int. Symp. Rinteln* 1966. pp. 273-281. Den Haag: Junk.
- PASSARGE, H., 1968. Neue Vorschläge zur Systematik nord-mitteuropäischer Waldgesellschaften. *Feddes Rept.* 77: 75-103.
- PASSARGE, H. & HOFMANN, G., 1964. Soziologische Artengruppen mitteleuropäischer Wälder. *Arch. f. Forstw.* 13: 913-937.
- PASSARGE, H. & HOFMANN, G., 1968. Pflanzengesellschaften des nordostdeutschen Flachlandes. II. *Pflanzensozilogie* 16: 1-298.
- PFEIFFER, H. H., 1957. Betrachtungen zum Homogenitätsproblem in der Pflanzensozilogie. *Mitt. Flor.-Soz. Arbeitsgem. N. F.* 6-7: 103-111.
- PFEIFFER, H. H., 1962. Über die Bewertung der Geselligkeitszahlen bei pflanzensozilogischen Aufnahmen. *Mitt. Flor.-Soz. Arbeitsgem. N. F.* 9: 43-50.
- PHILLIPS, J. F. V., 1931. Forest-succession and ecology in the Knysna Region. *Mem. Bot. Surv. S. Afr.* 14: 1-327.
- PIGNATTI, S., 1968. Die Inflation der höheren pflanzensozilogischen Einheiten. in TÜXEN, R. (ed.): Pflanzensozilogische Systematik. *Ber. Int. Symp. Stolzenau* 1964. pp. 85-97. Den Haag: Junk.
- POORE, M. E. D., 1955. The use of phytosociological methods in ecological investigations. I. The Braun-Blanquet system. *J. Ecol.* 43: 226-244. II. Practical issues involved in an attempt to apply the Braun-Blanquet system. *J. Ecol.* 43: 245-269. III. Practical applications. *J. Ecol.* 43: 606-651.
- POORE, M. E. D., 1956. The use of phytosociological methods in ecological investigations. IV. General discussion of phytosociological problems. *J. Ecol.* 44: 28-50.
- POORE, M. E. D., 1964. Integration in the plant community. *J. Ecol.* 52 (suppl.): 213-226.
- POORE, M. E. D., 1968. Studies in Malaysian rainforest. I. The forest on triassic sediments in Jengka Forest Reserve. *J. Ecol.* 56: 143-196.
- RAABE, E. W., 1952. Über den "Affinitätswert" in der Pflanzensozilogie. *Vegetatio* 4: 53-68.
- RAUNKIAER, C., 1934. *The life forms of plants and statistical plant geography*. Oxford: Clarendon.
- RAUSCHERT, S., 1963. Beitrag zur Vereinheitlichung der soziologischen Nomenklatur. *Mitt. Flor.-Soz. Arbeitsgem. N. F.* 10: 232-249.
- ROMELL, L.-G., 1925. Om inverkan av växtsamhällets struktur på växtsamhällsstatistikens resultat. *Bot. Notiser* 1925: 253-308.
- ROMELL, L.-G., 1926. Bemerkungen zum Homogenitätsproblem. *Svensk Bot. Tidskr.* 20: 441-455.
- ROBERTS, B. R., 1966. *The ecology of Thaba Nchu. A statistical study of vegetation/habitat relationships*. D. Agric. thesis. Pietermaritzburg: Univ. Natal. (Unpubl.).
- SCAMONI, A., PASSARGE, H. & HOFMANN, G. 1965. Grundlagen zu einer objektiven Systematik der Pflanzengesellschaften. *Feddes Rept. Beih.* 142: 117-132.
- SCHEEPERS, J. C., 1969. A preliminary assessment of association-analysis in the Kroonstad area. *Proc. Grassld. Soc. Sth. Afr.* 4: 78-83.
- SCHMID, P. & KUHN, N., 1970. Automatische Ordination von Vegetationsaufnahmen in pflanzensozilogischen Tabellen. *Die Naturwiss.* 57: 462.
- SCHMITHÜSEN, J., 1968. Allgemeine Vegetationsgeographie. in OBST, E. & SCHMITHÜSEN, J. (ed.): *Lehrbuch der allgemeinen Geographie*. 4. Berlin: De Gruyter. 3. Aufl.
- SCHWICKERATH, M., 1931. Die Gruppenabundanz, ein Beitrag zur Begriffsbildung der Pflanzensozilogie. *Bot. Jahrb.* 64: 1-16.
- SCHWICKERATH, M., 1944. Die Transformation konstant-methodisch erfasster Gesellschaften in die Charakterartenmethode und die Bedeutung und Gliederung des Differentialartenbegriffs. *Bot. Jb.* 73: 361-374.
- SCHWICKERATH, M., 1954. Lokale Charakterarten—geographische Differentialarten. *Veröff. Geotot. Inst. ETH, Stiftung Rübél* 29: 96-104.
- SCHWICKERATH, M., 1968. Begriff und Bedeutung der geographischen Differentialarten. in TÜXEN, R. (ed.): Pflanzensozilogische Systematik. *Ber. Int. Symp. Stolzenau* 1964. pp. 78-84. Den Haag: Junk.
- SEGAL, S., 1965. Een vegetatie-onderzoek van de hogere waterplanten in Nederland. *Wetensch. Meded. K.N.N.V.* 57: 1-80.
- SEGAL, S., 1969. *Ecological notes on wall vegetation*. Den Haag: Junk.
- SHIMWELL, D. W., 1971. *Description and classification of vegetation*. London: Sidgwick & Jackson.
- SPATZ, G. & SIEGMUND, J., 1973. Eine Methode zur tabellarischen Ordination, Klassifikation und ökologischen Auswertung pflanzensozilogischen Bestandsaufnahmen durch den Computer. *Vegetatio* 28: 1-17.
- STORY, R., 1952. A botanical survey of the Keiskammahoe District. *Mem. Bot. Surv. S. Afr.* 27: 1-184.
- SWAN, J. M. A., 1970. An examination of some ordination problems by use of simulated vegetation data. *Ecology* 51: 89-102.
- TAYLOR, H. C., 1969. *A vegetation survey of the Cape of Good Hope Nature Reserve*. M.Sc. thesis. Cape Town: Univ. Cape Town (Unpubl.).
- TIDMARSH, C. E. M. & HAVENGA, C. M., 1955. The wheel-point method of survey and measurement of semi-open grasslands and Karoo vegetation in South Africa. *Mem. Bot. Surv. S. Afr.* 29: 1-49.
- TUOMIKOSI, R., 1942. Untersuchungen über die Untervegetation der Bruchmoore in Ostfinland. I. Zur Methodik der pflanzensozilogischen Systematik. *Ann. Bot. Soc. Zool.-Bot. Fenn. Vanamo* 17: 1-203.
- TÜXEN, R., 1957. Die Schichten-Deckungsformel; zur Darstellung der Schichtung in Pflanzengesellschaften. *Mitt. Flor.-Soz. Arbeitsgem. N. F.* 6-7: 112-113.
- TÜXEN, R., 1969. Stand und Ziele geobotanischer Forschung in Europa. *Ber-Geobot. Inst. ETH, Stiftung Rübél* 39: 13-26.
- TÜXEN, R., 1970a. Entwicklung, Stand und Ziele der pflanzensozilogischen Systematik (Syntaxonomie). *Ber. Dtsch. Bot. Ges.* 83: 633-639.
- TÜXEN, R., 1970b. Pflanzensozilogie als synthetische Wissenschaft. *Meded. Landbouwhogeschool Wageningen* 12: 141-159.
- TÜXEN, R., 1970c. Einige Bestandes- und Typenmerkmale in der Struktur der Pflanzengesellschaften. in TÜXEN, R. (ed.): Gesellschaftsmorphologie. *Ber. Int. Symp. Rinteln* 1966. pp. 76-107. Den Haag: Junk.
- TÜXEN, R. & ELLENBERG, H., 1937. Der systematische und der ökologische Gruppenwert. *Mitt. Flor.-Soz. Arbeitsgem.* 3: 171-185.
- VAN DER MAAREL, E., 1966a. *Over vegetatiestructuren, -relaties en -systemen, in het bijzonder in de Duingrasslanden van Voorne*. Ph.D. thesis. Utrecht: Univ. Utrecht. (Unpubl.).
- VAN DER MAAREL, E., 1966b. Dutch studies on coastal sand dune vegetation, especially in the Delta Region. *Wentia* 15: 47-82.
- VAN DER MAAREL, E., 1970. Vegetationstruktur und Minimum-Areal in einem Dünentrockenrasen. in TÜXEN, R. (ed.): Gesellschaftsmorphologie. *Ber. Int. Symp. Rinteln* 1966. pp. 218-239. Den Haag: Junk.
- VAN DONSELAAR, J., 1965. An ecological and phytogeographic study of northern Suriname savannas. *Wentia* 14: 1-163.
- VAN VUUREN, D. R. J., 1961. *'n Ekologiese studie van die plantegroei van 'n noordelike en suidelike kloof van die Magaliesberge*. M.Sc. thesis. Pretoria: Univ. Pretoria. (Unpubl.).
- VAN ZINDEREN BAKKER, JR., E. M., 1971. *Ecological investigation on ravine forests of the Eastern Orange Free State (South Africa)*. M.Sc. thesis. Bloemfontein: Univ. O.F.S. (Unpubl.).
- VAN ZINDEREN BAKKER SR., E. M. & WERGER, M. J. A. 1973. Vegetation and phytogeography of the high-altitude bogs of Lesotho. *Vegetatio*: in press.
- VOLK, O. H. & LEIPPERT, H., 1971. Vegetationsverhältnisse im Windhoeker Bergland, Südwafrika. *J. S. W.A. Wiss. Ges.* 25: 5-44.
- VON GLAHN, H., 1968. Der Begriff des Vegetationstypes im Rahmen eines allgemeinen naturwissenschaftlichen Typenbegriffes. in TÜXEN, R. (ed.): Pflanzensozilogische Systematik. *Ber. Int. Symp. Stolzenau* 1964. pp. 1-14. Den Haag: Junk.
- WERGER, M. J. A., 1972. Species-area relationship and plot size: with some examples from South African vegetation. *Bothalia* 10: 583-594.
- WERGER, M. J. A., 1973a. *Phytosociology of the Upper Orange River Valley, South Africa. A syntaxonomical and syn-ecological study*. Ph.D. thesis Univ. Nijmegen. Pretoria: V. & R.
- WERGER, M. J. A., 1973b. An account of the plant communities of Tussen die Riviere Game Farm, O.F.S. *Bothalia* 11: 165-176.

- WERGER, M. J. A. & COETZEE, B. J., 1974. A phytosociological classification of Aughrabies National Park. *Bothalia* in prep.
- WERGER, M. J. A., KRUGER, F. J. & TAYLOR, H. C., 1972. Pflanzensoziologische Studie der Fynbos-Vegetation am Kap der Guten Hoffnung. *Vegetatio* 24: 71-89. also as: A phytosociological study of the Cape Fynbos and other vegetation at Jonkershoek, Stellenbosch. *Bothalia* 10: 599-614.
- WERGER, M. J. A. & LEISTNER, O. A., 1973. Vegetationsdynamik in der südlichen Kalahari. in TUXEN, R. (ed.): Sukzessionsforschung. *Ber. Int. Symp. Rinteln* 1973. Lehre: Cramer (in press).
- WESTHOFF, V., 1967. Problems and use of structure in the classification of vegetation. *Acta Bot. Neerl.* 15: 495-511.
- WESTHOFF, V., 1968. Einige Bemerkungen zur syntaxonomischen Terminologie und Methodik, insbesondere zu der Struktur als diagnostischen Merkmale. in TUXEN, R. (ed.): Pflanzensoziologische Systematik. *Ber. Int. Symp. Stolzenau* 1964. pp. 54-70. Den Haag: Junk.
- WESTHOFF, V. & DEN HELD, A. J., 1969. *Plantengemeenschappen in Nederland*. Zutphen: Thieme.
- WESTHOFF, V. & VAN DER MAAREL, E., 1973. The Braun-Blanquet approach of phytosociology. in WHITTAKER, R. H. (ed.): *Manual of vegetation Science*. 5. Den Haag: Junk.
- WHITTAKER, R. H., 1956. Vegetation of the Great Smoky Mountains. *Ecol. Monogr.* 26: 1-80.
- WHITTAKER, R. H., 1962. Classification of natural communities. *Bot. Rev.* 28: 1-239.
- WHITTAKER, R. H., 1967. Gradient analysis of vegetation. *Biol. Rev.* 42: 207-264.
- WILLIAMS, C. B., 1943. Area and number of species. *Nature* 152: 264-267.
- WITIGENSTEIN, L., 1960. *Philosophische Untersuchungen*. Schriften I. Frankfurt: Suhrkamp.
- WOODS, D. B. & MOLL, E. J., 1967. Multivariate analysis of grasslands in the Three Rivers area, Natal. *Proc. Grassld. Soc. Sth. Afr.* 2: 103-111.
- ZOHARY, M., 1973. *Geobotanical foundations of the Middle East*. Stuttgart: Fischer, and Amsterdam: Swets & Zeitlinger.
- ZONNEVELD, I. S., 1960. *De Brabantsche Biesbosch. Een studie van bodem en vegetatie van een zoetwatergetijden delta*. Ph.D. thesis. Wageningen: Landbouwhogeschool, Wageningen. (Unpubl.)