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(ACTON *et al.* 1960). The precipitation is approximately 15.5 inches (38.75 cm) of which approximately 6 inches (15 cm) falls during the summer. The soils are of the grey-wooded type, and generally belong to the «Waitville association» (MITCHELL *et al.* 1950). The region is part of the Mixedwood Section of the Boreal Forest (ROWE 1959).

The Swiss forests studied are located in the proximity of Roggwil, Langenthal (Kanton Bern) and Murgenthal (Kanton Aargau), between 47°21' and 47°16' latitude and between 7°48' and 7°54' longitude. They are situated on moraine deposits of the Riss period. The soils are mottled podzolized brown earths, and pseudogleys of the brown earth group (PALLMANN *et al.* 1943). The precipitation is approximately 116 cm of which 49% (56.8 cm)<sup>1</sup> occurs in the summer (MEYER 1949). These forests belong to the *Quercus-Abietetum* and partly to the *Melico-Fagetum* (FREHNER 1963). Some of these forests were described by Meyer as *Mastigobryeto-Piceetum abietosum* (MEYER 1949, 1954).

### 3. Nomenclature and terminology

The nomenclature of BINZ-BECHERER (1961) was followed for the *Pteridophyta* and the *Spermatophyta* in Switzerland. The nomenclature of BERTSCH (1959) was used for the Swiss *Musci*.

Where possible the nomenclature of FERNALD (1950) was followed for the Canadian *Pteridophyta* and *Spermatophyta*; elsewhere, RYDBERG'S (1954) nomenclature was followed. The nomenclature of GROUT (1928–1940) was used for the Canadian *Musci*, with the exception of *Calliergonella schreberi*, which is replaced by *Pleurozium schreberi* (Willd) Mitt.

The terms principal component, principal factor, and principal axe have the same meaning. The term factor, however, can easily be mistaken in ecological work for a habitat factor, which it is not. Therefore, the term principal factor is not used in this publication. The term factor is used exclusively in the sense of habitat factor. Wherever other features of these habitats or plant communities were included in the analysis (e.g. height-growth of the white spruce trees, nitrogen content of the white spruce foliage) the term features is used.

### 4. Theoretical considerations

Investigations of the ecology of vegetation can be divided into three stages (ELLENBERG 1954):

- (1) Description;
- (2) Organization (ordination and classification);
- (3) Interpretation.

#### 4.1 Description

A sample consists of a small portion separated from some large population, about which certain information is sought. The problem is to gather adequate

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<sup>1</sup> 116 cm = 46 inches, 56,8 cm = 22,6 inches

information from each vegetation-type and each sample plot, to detect significant, rather than accidental, trends and differences. This raises the question of delimitation of sample areas, sampling units and number of samples to collect. If too many data are collected, this generally lowers the quality both of the important and of the unimportant data. Certain rules can and must be set up to enable the field worker to decide without much difficulty, whether a sample belongs to the population to be sampled.

In order to contain reliable information about the population, each member of the sample (sampling unit and sample plot) must be selected *at random*.

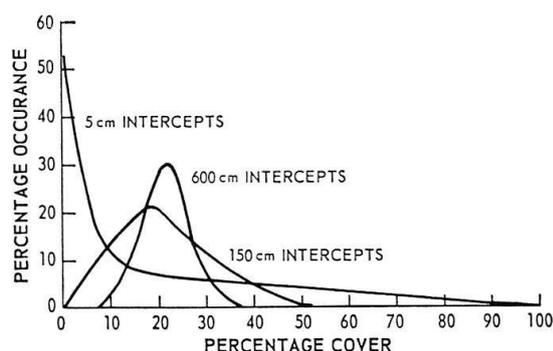


Fig.1. Smoothed frequency curves indicating the increasing normality of the distribution of the cover percentages with increasing length of line-intercepts.

This random selection implies that each point within the sampling area has the same chance of appearing in the sample.

With a normally distributed estimate, the whole shape of the frequency distribution is known, if information is available about the mean and the variance. If the individuals or groups of individuals are not distributed at random, and if the sampling unit is approximately of the same size as the individuals or groups of individuals, the frequency distribution of the estimate of the cover percentages is not normal.

In several instances, it has been found that non-random patterns of different scales can be present simultaneously in one vegetation-type (GREIG-SMITH 1961, KERSHAW 1958, 1959).

It is important that the vegetation data contain information about the spatial distribution of the plant species of each sample plot, for the following reasons: (1) From the statistical point of view, it is desirable that the size of the sampling unit be such that, (a) the data are normally distributed (Fig.1), because then the shape of the frequency distribution is known, if the mean and the variance are known and, (b) the variance is relatively little affected by small deviations in the size of the sampling unit (see Figs.8 and 9). (2) If

a small scale non-random pattern within the sample plot is present, this can be investigated and elucidated. When the material is far from uniform, as in vegetation studies, the method by which the sample is obtained is crucial and the study of techniques that insure an adequate sample becomes important. Different sampling techniques should be tested for efficiency. One way of fulfilling the combined requirements is by a method first proposed by GREIG-SMITH (1952) and later refined by him and Kershaw, the use of contiguous quadrats or other contiguous systematic samples (point-quadrat-line, line-intercept, KERSHAW 1958).

#### 4.2 *Organization (ordination and classification)*

The basic task of organizing vegetation data is to simplify them, so that a relatively simple model of the vegetation emerges. This simplification can, of course, only be successful if the distribution of the species is governed by a few factors of overriding ecological importance, or if the quantities of certain species on the various sample plots are correlated. To attain the above goal, many different approaches were developed.

One of the most widely used methods is that of the Zürich-Montpellier School. As the result of the recognition of the limited usefulness of the "characteristic species" concept, the methods employed by the disciples of this school to differentiate between the various plant community-types have gradually developed towards the use of the differential species-group (SCHÖNHAR 1953, ELLENBERG 1956, SCHLÜTER 1957, FREHNER 1963).

Each differential species-group is made up of species which occupy identical, or nearly identical, ranges within moisture, pH and other gradients (SCHLÜTER 1957, p.48). ELLENBERG (1963 p.84) presents an elaborate scheme of the species-groups of the forest plants of Central Europe. The sample plots are then classified according to the occurrence of these species-groups. A classification based on the occurrence of species belonging to these differential groups, of course, does not need to assume a basic discontinuity in the pattern of distribution of the vegetation as a whole, as has often been implied by critics of the Zürich-Montpellier school. It divides the vegetational catena into segments, which are typified by the presence or absence of the species belonging to these differential groups.

As a result of the development of large and fast electronic computers, it has become feasible to make use of multivariate statistical methods, such as factor analysis, discriminant analysis and Mahalanobis' generalized distance, to organize phyto-sociological and ecological data.

A concept which is fundamental in considering many variables together is

the test-space. If measurements have been made of the cover (or any other attribute) of  $m$  species on  $N$  sample plots, the data can be presented in matrix form as follows:

Plot \ Spec.	1	2	.....	N
1	$x_{11}$	$x_{21}$	.....	$x_{N1}$
2	$x_{12}$	$x_{22}$	.....	$x_{N2}$
⋮	⋮	⋮		⋮
$m$	$x_{1m}$	$x_{2m}$	.....	$x_{Nm}$

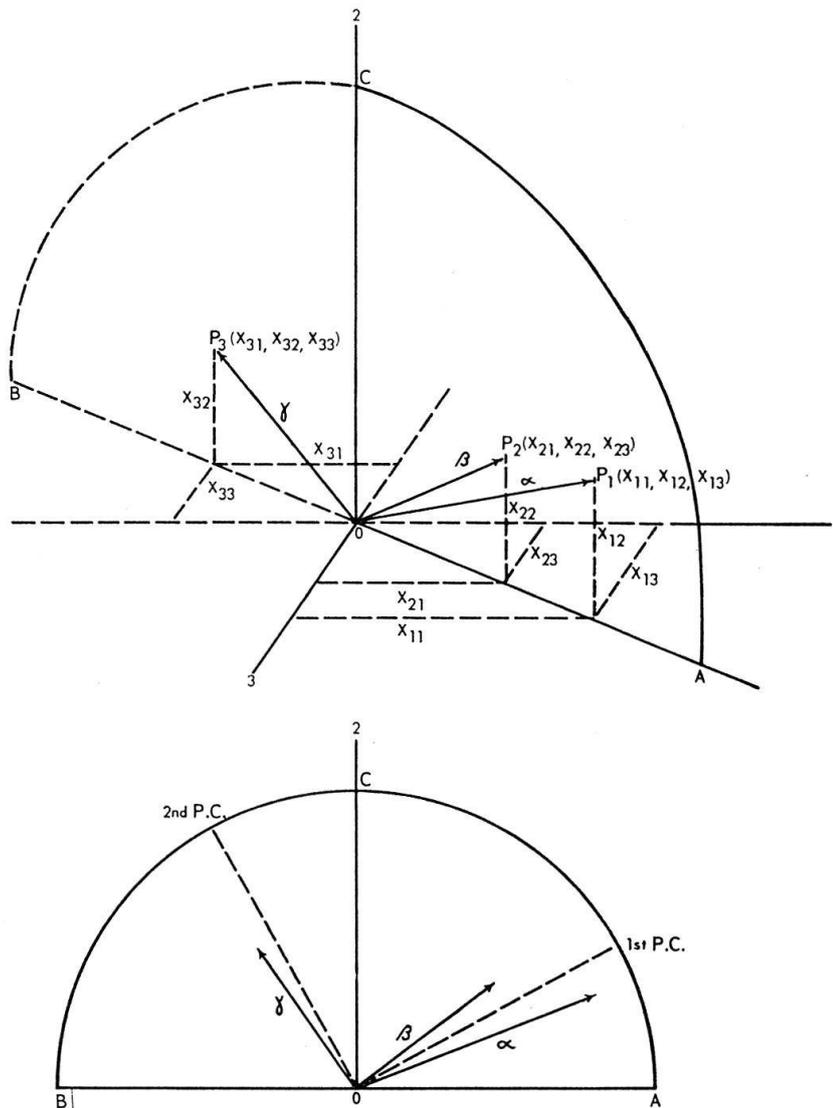


Fig. 2. Top: Vector representation of plant species (explanation in text). Bottom: Principal components (P.C.) of above vector representation.

These data can be presented geometrically in the forementioned test-space in two different ways:

(1) *The vector representation.* Each species is represented by one vector (see appendix V) in an N-dimensional test-space (as many axes as there are sample plots). Each vector is determined by two points: the origin of the test-space, and the end point of the vector, which is determined by an ordered set of coordinates, e.g. for species 1 ( $x_{11}, x_{21}, \dots, x_{N1}$ ). The cosines of the angles between the vectors are equivalent to the coefficients of correlation between the respective species. A three-dimensional example is presented in Fig.2. For the sake of simplicity the vectors denoted by  $\alpha$ ,  $\beta$  and  $\gamma$ , representing species 1, 2 and 3, are shown as lying in one plane ABC.

The interpretation of an  $m \times m$  matrix of indices, expressing relationships between species, is the vector representation. The test-space involved will be referred to later to as the R-space.

(2) *The point representation.* Each sample plot can be represented by one point in an m-dimensional test-space in which each axis represents one species (m species = m axes). So plot 1 is represented by the point having the following coordinates ( $x_{11}, x_{12}, \dots, x_{1m}$ ). There are thus N points representing N sample plots in an m-dimensional test-space. Fig.3 is an example of the point representation of two sample plots containing three species 1, 2 and 3. On plot 1 the species have the following cover percentages 20, 15 and 10, respectively; on plot 2 these percentages are 6, 7.5 and 5 respectively. The interpretation of an  $N \times N$  matrix of coefficients of similarity between sample plots is the point representation. The test-space involved will be later referred to as the Q-space.

In the case of the vector representation, the first problem arising is the choice of the most efficient statistic of interspecific relationship. Many workers have discussed these coefficients but the most complete account has been presented by DAGNELIE (1960). Statistics expressing interspecific relationships can be based on either qualitative or quantitative data. In both cases, the statistics are sensitive to changes in size of the sampling units. Until now, this fact has received little attention in ecological literature, but it should not be neglected (KERSHAW 1961).

Further, interspecific association coefficients are sensitive to enlargement of the study area, where the added areas are devoid of one of the species under consideration (BRAY 1956). They are, thus, most useful when the vegetation samples are fairly similar. Some ecologists believe that various species respond in the same way to various combinations of different levels of habitat factors, thus obscuring the habitat relationships. This possibility increases when a wider range of conditions is sampled. The narrower the range of habitats

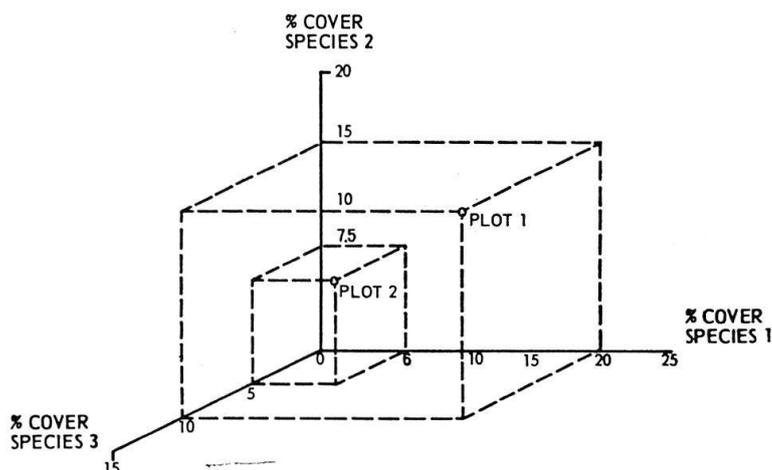


Fig. 3. Point representation of sample plots (explanation in text).

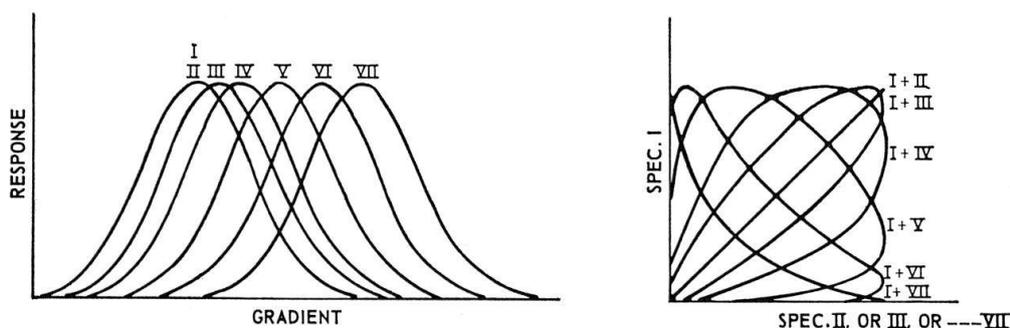


Fig. 4. Top: Hypothetical gradient response curves of seven species at six different ranges along gradient. Bottom: Graphical representation of the quantitative relationships of species I with the other six species.

sampled, the closer the relationship between the vegetation and the habitat can be expected to be.

The quantitative relationships between species are very complex. Consider, for instance, the relationship between a number of species all of which have identical bell-shaped response curves along an ecological gradient (gradient response curves), but which are occupying different ranges along the gradient (Fig. 4, top). These are much simplified situations which are highly improbable in nature, but which can illustrate the problems under consideration. Graphically, the quantitative relationships between each pair of species can be shown by plotting the quantities of the two species occurring at each point along the gradient, on a pair of orthogonal axes, each axis representing one species (a two-dimensional test-space). The result is a very artistic family of curves (Fig. 4 bottom), each curve representing the relationship between two species. If the species occupy the same range (e.g. species I and II), the curve

representing the relationship between the species is a straight line. The curves representing the relationships between species, which occupy ranges which overlap to a lesser degree, e.g. species I and III, or I and IV, are more egg-shaped. When the ranges overlap even less, the curves become triangular finally to change to parabolic shapes. Attempts made by this author to develop a single formula which satisfactorily describes these relationships were not successful. In nature several ecological gradients can be expected to act concurrently. Some of these may be correlated; others not. Further, all shapes of response curves may be expected, especially where species affect one another (ELLENBERG 1953, 1956, 1963). Clearly the foregoing example is very much simplified.

By assuming linear relationships between species, valuable information may be lost, but as far as this author is aware, no mathematical methods based on curvilinear relationships have been developed. An examination of forementioned curves, however, reveals that, if sampling is restricted to a narrow range of conditions (a small piece of the gradient), the relationship between the species can be represented by a short segment of the curve, thus more closely approaching linearity. Thus, in order that the interspecific-association indices (or indices expressing relationships between vegetation samples) will yield as much information about habitat and interspecific relationships as possible, the range of habitats to be sampled should be kept fairly narrow.

After the choice of the statistic of interspecific relationship has been made, two basic problems arise:

(1) Is it possible to replace the initial  $N$  axes in the original test-space by a few variables (components), which account for practically all the variance? The answer depends on the correlations between the species (angles between the vectors). If the  $m$  vectors can be divided into groups of vectors, in such a manner that within a group the angles between the vectors are small, but with large angles between the vectors of different groups, the replacement of the  $N$  axes by a small number of new, mutually orthogonal, components (as small a number of components as there are groups of vectors) should be possible. This is accomplished by principal component analysis.

A simple geometrical illustration of the replacement of a number of axes by two components is presented in Fig. 2. This concept can be considered a refinement of the differential species-group concept. Whereas the species-group rests on the co-occurrence of certain species, the component is determined by the quantitative relationships (both positive and negative) among species.

(2) In the event that mutually orthogonal components have been found, it still remains to be determined whether they are ecologically significant.

This, however, is a matter of interpretation, which will be dealt with in the section under that heading.

If mutually orthogonal components can be found and estimates of the amount that each species contributes to the various components are available, it is then possible to calculate the coordinates of each plot along the components by multiplying the quantity of each species by its corresponding coefficient and summing these new values. The result is an ordination of the sample plots in the new test-space as delineated by the components, or in other words, *through a vector representation of the species, a point representation of the sample plots is obtained.*

The following question now arises: Do the points in the new space form a set of clusters? There is no unique way in which a cluster can be defined. The judgement of the research worker forms the ultimate criterion in the appraisal of the value of these definitions. In this study a cluster is defined as a group of samples, within which the samples are more similar to one another than to vegetation samples outside the cluster. A cluster would represent a unit in a classification system.

To determine whether the points form clusters, different methods can be employed. If only a few clusters are involved, an examination of the projections of the points, representing sample plots, on the planes spanning the components is adequate. If this is not satisfactory, other methods are available, most of which require the calculation of the distances between the points in the new test-space. This is easily accomplished using the Pythagorean theorem. One method of cluster analysis, based on the distances between the points, will be discussed later.

Most ecologists, who have determined measures of quantitative interspecific relationships, have not tried to analyse these data statistically. GOODALL (1954) and DAGNELIE (1960) used factor analysis to analyse matrices of interspecific correlations. GOODALL observed indications of clustering (a bimodal distribution) along the first principal axis in the frequency distribution of the values of the various sample plots. No cluster analysis in the strict sense, however, was made to investigate the grouping of the sample plots.

Of the different methods of factor analysis available, to determine if the original variables can adequately be replaced by a few components, mathematically the most robust method is principal component analysis, as first developed by HOTELLING (1933).

IHM (1964) developed a computer program, for principal component analysis of covariance matrices, which is particularly suited for vegetation analysis. It does not only compute the trace (= sum of all eigenvalues), the

eigenvalues, and the eigenvectors of the covariance matrix (see appendix V) but also calculates, for each sample plot, the value of each component (the coordinates of each sample plot) and plots the projections of the points, representing the sample plots, on the planes spanning the first and second axes, and the first and third axes. The eigenvalues indicate the relative importance of the species combinations (principal components), represented by the coefficients of the associated eigenvectors. From the eigenvalues it is possible to calculate the percentage of the total variation accounted for by each component (see appendix V). The species that have large coefficients, contributing to the eigenvectors, are said to be causing most of the variation represented in the eigenvalue.

In the case of the point representation, the first problem to be solved is the choice of the statistic expressing the similarity (or dissimilarity) between the vegetation samples. As DAGNELIE'S review (1960) clearly shows, many different indices, expressing similarities between vegetation samples, have been proposed. It is obvious that similarity indices based on quantitative measures are more sensitive than those based only on presence and absence data<sup>1</sup>. Practically all quantitative similarity indices, however, suffer from some imperfections. Most of these indices increase rapidly with an increase in the number of species. It is not easy to determine from the changes in similarity index whether the newly added species supply additional information for the purpose of classification or ordination. If the quantities (percentage cover) of the species on two sample plots are used to calculate a similarity index which, it is hoped, will also express the similarity in habitat, and if the species are quantitatively correlated, a non-orthogonal comparison is being used, in other words the axes in the test-space are not mutually orthogonal. If the species are positively correlated (e.g. they react more or less similarly to differences in habitat, or the presence of the one species favors the growth of another species), then the similarity index indicates a greater similarity (a smaller distance) between the vegetation samples than where the species are not correlated. This phenomenon is geometrically illustrated in Fig.5. Assume that points  $P_1$  and  $P_2$  represent two sample plots. The quantities of species A and B on plot 1 are respectively  $a_1$  and  $b_1$ , and on plot 2 respectively  $a_2$  and  $b_2$ . The species A and B can each be represented by one axis in a two dimensional test-space. If the species are quantitatively not correlated, the axes are mutually orthogonal. The distance (D) between  $P_1$  and  $P_2$  can now be calculated with the help of the Pythagorean theorem:  $D^2 = (a_1 - a_2)^2 + (b_1 - b_2)^2$ . If, however, the species A and B<sup>1</sup> are quantitatively correlated,

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<sup>1</sup> Recent work by LAMBERT and DALE (Adv. ecol. Res. 2, 1964) indicates that this may not always be true.

the axes are not orthogonal but oblique. The cosine of the angle between the axes, in this case, is equal to the correlation coefficient. If we assume that the correlation coefficient is .682, then  $\cos \alpha = .682$  and  $\alpha = 47^\circ$ , and the position of  $P_1^1$  and  $P_2^1$  can be constructed. Assuming the quantities for species A and B<sup>1</sup>, as before, the distance between  $P_1^1$  and  $P_2^1$ ,  $D^1$ , is obviously smaller than  $D$  ( $D^1 = \text{appr. } .85 D$ ). If the species are negatively correlated, the distance is greater than when the species are uncorrelated.

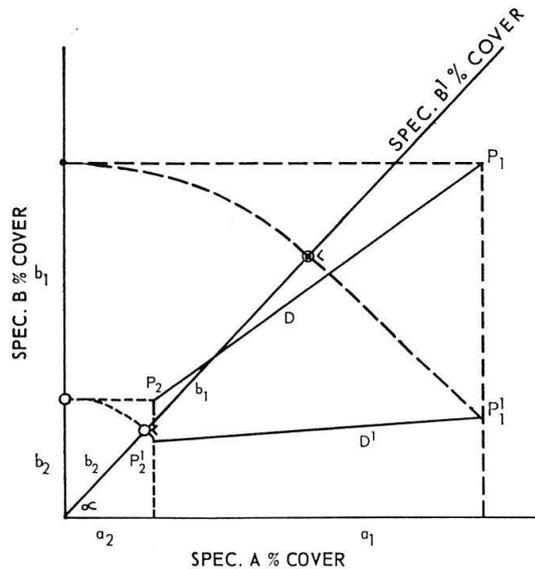


Fig. 5. Distance  $D$ , if species quantities are not correlated, compared to distance  $D^2$  when the correlation coefficient between the species is .68 ( $D = 1.18 D^2$ ).

The problem created by the quantitative correlations between species is taken care of by the  $D^2$  statistic. This statistic was first proposed by MAHALANOBIS (1936) and used by him and co-workers (MAHALANOBIS *et al.* 1949) for comparisons between ethnic groups in India. HUGHES (1954), first applied it in plant ecology to test the differences between groups of sample plots, which had been established by criteria other than the vegetation. The  $D^2$  statistic is used in this investigation as an index of dissimilarity between separate sample plots.

The  $D^2$  statistic is a *measure of distance* (reciprocal of similarity), rather similar to the more familiar Student's "t". In fact the  $D^2$  reduces to the "t" if comparisons are made with one variable only. The  $D^2$  statistic, also called Mahalanobis' "generalized distance", is best illustrated by a geometrical figure (Fig. 6).

For example, suppose the dissimilarity between two sample plots (stands) is to be calculated. For the sake of simplicity, presume that only two species

are present (A and B, Fig. 6). On plot 1, species A has a mean cover, expressed in standard deviation units, of  $a_1$ ; on plot 2, the cover is  $a_2$ . On plot 1, species B has a mean cover of  $b_1$ ; on plot 2, the cover is  $b_2$ . The location of each plot in two-dimensional space is fixed by the coordinates,  $a_1$  and  $b_1$  for plot 1, and  $a_2$  and  $b_2$  for plot 2. The distance between plot 1 and 2 can now be calculated using the Pythagorean theorem,

$$D^2 = (a_1 - a_2)^2 + (b_1 - b_2)^2.$$

These  $D^2$ 's can be tested for significance.

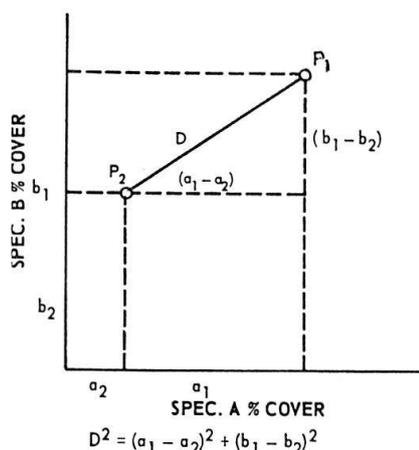


Fig. 6. Distance between two sample plots in two-dimensional space (species not correlated).

The method can be extended for 3, 4, or more species by adding mutually orthogonal axes to the two originally used, one axis for each species added. The formula for  $D^2$  now becomes,

$$D^2 = (a_1 - a_2)^2 + (b_1 - b_2)^2 + (c_1 - c_2)^2 + (d_1 - d_2)^2 + \dots$$

This formula is valid only if the variables (quantitative measures of species) are not correlated.

If the variables are correlated, as is usually more or less the case with different species, they can be replaced by a set of transformed variables, which are linear functions of the observed variables and are mutually uncorrelated (MAHALANOBIS *et al.* 1949; see also appendix IV). The location of each plot is now fixed in multidimensional space (as many axes as there are species) and the distances between these plots and their probability levels are known.

It seems opportune to discuss at this point the different concepts held by various ecologists on the structure and spatial distribution of plant communities.

Although recognizing the continuous nature of vegetation (EHRENDORFER 1954), most of the European-schooled workers, for practical purposes, assume in most cases a non-random pattern or actually a pattern closely enough resembling a non-random pattern that no large errors are made. How close this assumption approaches reality, however, is seldom proved by showing: (1) actual discontinuity in the vegetation or of the habitat factors; or (2) statistical meaningful differences between the classification units in vegetation or levels of habitat factors. The methods developed and used for grouping vegetation samples result in the division of the vegetation into segments, which may or may not coincide with significant different levels of the habitat factors or site features.

ELLENBERG (1956) showed how indices of stand similarity based on species quantities, (Massen-Gemeinschaftskoeffizienten) can be used to verify the grouping of vegetation samples.

Much of the work done by ecologists of the Wisconsin school is based on the assumption that all patterns, except the largest scale patterns, are random. Different parts of the vegetational pattern form a so called continuum. A method was developed called a continuum analysis in which "adaptation numbers" (a sort of coefficient of interspecific relation, determined from a matrix of indices of amplitudinal correspondence (BRAY 1956), were used to calculate a "Continuum Index" (C.I.) for each stand-sample. The C.I. is used to ordinate stands along an ecological syndrome or continuum. As such, the C.I. can be classified under the statistics expressing relationships between vegetation samples. The quantitative distribution of species along the continuum showed continuous and interchanging patterns. The conclusion was drawn that this proves the non-existence of distinct plant community-types (associations, forest-types etc.).

MAYCOCK (1963), after grouping sample plots according to moisture classes, came to the same conclusion. He states: "When the forests were grouped together on the basis of their site moisture features and importance values for individual component trees were averaged for all the five classes, it was clearly shown that each tree has a graded specific relationship in response to the grouping or ordering of stands. When the assemblages of tree responses were considered as a whole it was evident that a forest continuum is existent (at least within the tree layer). Specific distinct forest communities are either a figment of the imagination or those segments of forest composition on particular portions of the environmental moisture series that an investigator has chosen for specific research investigations". (MAYCOCK 1963, p.424-425). Other ecologists working along the same lines have made similar statements (BRAY *et al.* 1957, CURTIS 1959).

These studies, however, elucidate only the relationships between species and between species and habitat factors, and do not take into account the spatial distribution of the different communities. If an area that is covered by a non-randomly distributed vegetative cover is sampled at random, the samples can be placed in groups in such a manner that, in each group, the samples are more similar to one another than to samples outside their group, and yet an analysis of the type mentioned before will not show discontinuity in the quantitative distribution along gradients, but unbroken, smoothly intergrading patterns.

A non-random distribution at different levels of occurrence, can have different causes: (1) morphological properties of the species; and (2) non-random distribution of the different levels of the controlling habitat factors.

Most ecologists have considered only the co-occurrence of species as a basis for classification. BRAY (1956) states: "The floristic basis of community classification, both European and American, is dependant upon the fact that certain species tend to occur together". The spatial aspects of vegetation distribution, however, should definitely be a major part of the considerations.

It is quite possible that individual species have smoothly graded response curves over a wide range of several gradients, with their optima at different positions along the gradients. Yet, classification is possible, because the spatial distribution of the different levels of the habitat factors (and as a result that of the vegetation as a whole) is not random. This can be shown by studying the frequency distribution, if the sample plots can be adequately ordinated along one axis (one-dimensional space), or by cluster analysis if the plots are ordinated along several axes (multidimensional space).

If groups have been established in another manner, e.g. as was done by МАУ-ЦОК (1963), using moisture classes, these groups can be tested for vegetational differences by multivariate methods, e.g. Hotelling's T or Mahalanobis'  $D^2$ .

The next problem to be solved, is whether the points in the forementioned multi-dimensional space form clusters. Several types of cluster analyses are possible. One of the simplest was, according to Rao, suggested by Tocher (RAO 1952). The principle is as follows: One starts with two plots which are most similar and finds a third plot which is closest to the first two, by determining which has the smallest average distance from the first two plots. The fourth plot is chosen by determining the smallest average distance from the first three plots, etc., etc. If at any stage the average distance increases substantially, (this is a subjective criterion), the last plot is considered not to belong with the group of sample plots that has been processed. The data of the group in question are removed from the general set and the rest is treated as before (Appendix III).

In cases where the vegetation is continuously variable, in other words, where all samples form one cluster, the investigator is left with a constellation of points in multi-dimensional space, which cannot be utilized in this form. The possibility, however, remains that the variation within the set of vegetation samples can be adequately explained by a few variables instead of the original large number  $m$ . These new variables may or may not be related to ecological features.

This problem can be attacked by different ordinating techniques. Two procedures can be followed. The first originated with TORGERSON (1952) and was used with apparent success by BRAY and CURTIS (1957) in their ordination of upland forest communities of southern Wisconsin. They have described this method in detail: "This technique depends upon the selection of a pair of reference stands for the determination of stand positions on any one axis. Given proximate interstand distances, the choice of reference stands is of crucial importance. In making this choice it is evident that reference stands are comparable, in part, to sighting points as used in plane table surveying and that those stands which are furthest apart will be more accurate for judging interstand distances than those in close proximity".

"It is necessary for any ordination that the sphere of fluctuation for any stand be small in relation to the space occupied by the ordination as a whole. The choice of reference stands should be, therefore, of those stands which are furthest apart, and as a consequence, have the greatest sensitivity to overall compositional changes".

"To locate stands between a pair of selected reference stands, a line connecting the reference stands is drawn to scale on a piece of blank paper and the position of each other stand is projected onto this line. The projection is accomplished by rotating two arcs representing the distance of the projected stand from each of the reference stands and then projecting the point of arc intersection perpendicularly onto the axis".

"A second axis can be constructed by the same method, using a line on the paper erected at a right angle to the X axis. Two new reference stands are selected which are in close proximity on the X axis, but which are nevertheless separated by a great interstand distance".

There are, however, some drawbacks to this procedure. Where the relationships between a great number of plots are being analysed, the method becomes rather laborious. A disadvantage of this procedure is also the burdensome method used to obtain a measure of the total variation accounted for by the axes determined. At each stage the distances between the points are compared with the distances in the original matrix, and the correlation coefficients calculated.

A mathematically more sophisticated procedure is the “Q” method of factor analysis as used by DAGNELIE (1960), in particular that method of factor analysis called “principal component analysis”. In this case (see appendix V) principal component analysis, also called the method of principal axis or principal factors, investigates whether the information conveyed by all the “generalized distances” between the plots may be adequately represented by fewer variates, which may be used in place of the original variates (the species quantities).

The  $D^2$ 's (a distance measure) as such, however, cannot conveniently be analysed by principal component analysis. For this analysis, the  $D^2$ 's preferably should be transformed into indices of similarity (R). The simple reciprocals should not be used, because they have the same theoretical limits as the  $D^2$ 's, 0 and infinity.

Two transformations, which can be used were suggested by Ihm<sup>1</sup>:

$$\begin{aligned} \text{a) } R_1 &= e^{-D^2} \\ \text{b) } R_2 &= (1 + D^2)^{-1} \end{aligned}$$

Either transformation can be used, because the limits of both of the new indices vary between 0 and 1, from complete dissimilarity to complete similarity.

In geometrical terms, the plots, represented by points in a multidimensional coordinate system, form a constellation of points of an hyper-ellipsoidal form. The principal component method finds the so-called principal axes of this hyper-ellipsoid, and projects the forementioned points on these. It determines first an axis along which the variance is maximum, and second an axis, at right angles to the first axis, along which the remaining variance is maximum etc. etc. Theoretically, there are as many principal axes as there were axes in the original test-space, but usually a large proposition of the total variance is accounted for by the first few (3–5) axes. This represents a convenient simplification of the original N variables. For a geometrical representation of the reduction of a three-dimensional to a two-dimensional test-space, see Fig.7. For the sake of simplicity, assume that all points are lying in the plane through A, B and C. The original three axes can then be replaced by two new axes, going through the centre of gravity of the group of points, P, and lying in the plane A B C. These axes are the principal components sought. The method supplies the trace of the matrix (= sum of all eigenvalues), the “eigenvalues” and the “coefficients contributing to the eigenvectors”. The eigenvalues give a quantitative indication of the relative

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<sup>1</sup> Personal communication.

importance of each axis. From the eigenvalues and from the trace, it is possible to calculate the percentage of the total variation accounted for by each axis (see appendix V). The coefficients of the eigenvectors contributing to the eigenvalues denote the coordinates of the points in this “component space”.

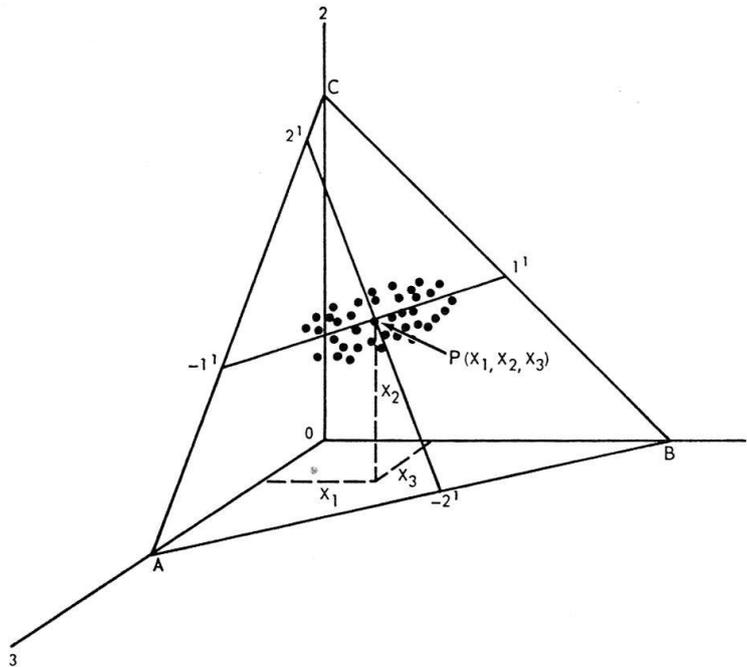


Fig. 7. Hypothetical ellipsoid shaped cluster of sample plots in three dimensional space with principal components (explanation in text).

### 4.3 Interpretation

The differential species-group concept postulates that the species belonging to such a group are present in the vegetation over a limited range of levels of certain habitat factors. It is then to be expected that a grouping of sample plots, based on this concept, results in community-types which occupy different ranges along various environmental gradients e.g. the soil moisture and pH gradients.

Associated with these different ranges along environmental gradients, one expects to find significantly different levels of one or more other site features e.g. height-growth of the various tree species, reproductive power of these species, disease susceptibility, etc.

If the sample plots have been grouped according to above-mentioned method, it remains to be decided to what extent the aim of the method has been accomplished. To this end, the habitat and other data can be subjected to statistical tests. FREHNER (1963) used the “t” test to investigate the signi-

ficance of the differences in average height, reached at an age of 100 years, of several tree species in the community-types distinguished by him. VAN GROENEWOUD (1965) used the "t" test to compare the mean levels of both habitat and other site features in various community-types. With respect to the separation of different ranges along environmental gradients, however, the "t" test is not very discriminative. It should be realized that if sufficient measurements are made on each sample plot, very small differences between the mean values of the various plots will almost always be statistically significant. The mean levels of two ranges along an environmental or other gradient can be highly significantly different ( $P \leq .001$ ) yet the ranges may almost completely overlap. A more satisfactory criterion for the relative separation of different ranges would be the ratio of the difference between the mean levels,  $\Delta$ , to the sum of the standard deviations  $\sigma_1 + \sigma_2$ :

$$(\Delta / \sigma_1 + \sigma_2).$$

The outcome of the vegetation analysis, can take three possible forms:

(1) The points, representing sample plots or stands in either the R or Q space, form a cluster of hyper-spherical shape. No classification or ordination of practical value can be made. In the principal component analysis, this would result in a number of eigenvalues which vary little in size.

(2) The points do not form separate clusters, but one cluster of hyper-ellipsoid shape, the axes of which can be determined. These axes form the ordinates of an ordinating system.

(3) The points form a number of clusters. These clusters are equivalent to units in a classification system.

In the latter case, classification is a possibility, but not a necessity. The choice between classifying or ordinating depends on the requirements of the investigator.

There are no indications, so far, that the possibility mentioned under 1 is other than theoretical. It is doubtful whether it actually occurs in nature. If it does occur, a different approach to vegetation analysis could be used (e.g. gradient analysis). This will not be further considered here.

After extraction of the principal components, the ecological meaning of these components can be elucidated. The principal component analysis of the matrix of coefficients expressing relationships between plots (the point representation) can be interpreted in ecological terms as follows: the points, representing the sample plots, form a swarm (constellation or cluster) of as yet undefined shape in the original test-space. If we assume that the points form a swarm of hyper-ellipsoid form, the points (plots) farthest apart are the most dissimilar in floristic composition. It can be reasoned that this is not the

result of chance, but that this dissimilarity is caused by a concurrent dissimilarity in the habitats. It can be postulated that the axis which joins these extremes does represent a gradient of intermediate habitat conditions (usually a set of correlated habitat factors). The forementioned axis, however, represents only the variability in one direction. The reasoning in explaining the variability along the second axis is analogous to that for the first axis.

Several authors (GREIG-SMITH 1964, GOODALL 1954) have already pointed out that the principal components (R-method) do not necessarily represent ecological factors, but are strictly expressions of relationships between the quantities of the species. It can be reasoned, however, that these relations are not just the result of chance, but are more or less caused by the fact that species are affected in the same or dissimilar manner by particular sets of habitat factors, or by the effect that one species has on the performance of the other. It should then be possible to decompose the covariances among the species into a small number of orthogonal components, each comprising a set of species, which have high covariances among them. Theoretically then, these components should be correlated with habitat factors, or better, with sets of correlated factors.

To test the hypothesis that the principal components are related to habitat features, the various levels of each habitat feature can be related to the corresponding values of the principal component (projections on the axes = coordinates). In order to avoid much unnecessary work, the level of each habitat feature for each plot can first be plotted against the corresponding values of each plot for each component, to determine if any relationship, linear or curvilinear, is present. If the graph indicates the likelihood of a relationship, this relationship can further be defined by fitting a straight line or a curve to the data.

Because the axes are perpendicular to each other, it is to be expected that, if relationships are detected, the different axes are related to habitat factors which operate independently of each other.

The habitat factors can also be included in the principal component analysis. This, however, in most cases is not desirable because these factors would also contribute to the ordination of the plots, even in cases where no actual causal relationship exists among the factors included and the distribution of the vegetation.

In the case of clustering, as in grouping according to the differential species-group method, it remains to be decided if the clusters also have ecological significance. In other words, it must be determined if the groups, besides being vegetationally different, are also significantly different in habitat.

To establish this, first the ecological meaning of the principal axes is considered. It is unlikely that significant differences could be obtained between the means of the levels of a habitat factor on various plots, if the habitat factor is not related to one of the principal axes of the ordination. The reverse is not true. This depends on the type of relationship between the principal axes and habitat factors and on the relative position of the clusters with respect to the principal axes.

Where more than two groups are involved, if the number of measurements of the habitat factor are the same for the groups to be compared and if the variances are not markedly different, the differences between the means can be tested by variance analysis. Otherwise, "t" tests with corrections for different numbers of samples and for differences in variance are indicated (GREIG-SMITH 1964, p.35).

In case the analysis of variance in relation to the length of line-intercept, or in relation to quadrat size, does not indicate a non-random pattern in the species distribution of the sample plot, the possibility still exists that a causal relationship between vegetation distribution and habitat factors does exist, if both are distributed at random. Within the sample plots, the variation in the levels of most habitat factors is small. There are, however, a few factors which can form random patterns in small areas, within which the levels can vary considerably. One such factor is light. If a non-random vegetational pattern can not be shown to exist, the forementioned case would be analogous to that in the  $D^2$  analysis, where no grouping can be discovered, and yet the distribution of the species is affected by factors as indicated by the principal component analysis. This problem could be solved by the use of principal component analysis. The labor that would be involved makes this an impractical approach.

A quicker method is to plot the level of the habitat factor concerned as measured along the line-intercepts, directly against the percentage cover of each species, as measured in each section of the line intercept (Fig.12). Relationships, if any are present, will be evident in the graphs.

#### 4.4 *General considerations*

In judging the relative merits of different methods for ordinating and classifying vegetation samples, the following should be considered:

(1) The method must result in the *simplest possible* ordering of the vegetation samples which should account for the *largest possible* portion of the variation within these samples.

(2) Both the ordination and the classification should preferably be related to habitat factors;

(3) Ideally, the method should be based on a statistic which forms both an objective criterion to determine whether classification is possible, and a basis for an ordination, which can be used as an alternative in describing the vegetation, in case it is continuously variable,

(4) The method should furnish a means of placing newly measured vegetation samples in a previously derived ordination or classification system, without going through the whole analysis each time; and

(5) If the objectives of 1 and 4 can be accomplished, it should then be possible to devise a system that will allow the mapping of vegetation samples which tend to form a continuum. This would greatly increase the usefulness of the method.

## 5. Methods

### 5.1 *Vegetation*

#### 5.1.1 Sampling

Location of sample plots.

As mentioned before, ideally the samples should be located at random. In practice, however, this is subject to limitations. In locating the sample plots, the following conditions were adhered to: (1) Each sample plot with surrounding area should be undisturbed; (2) it should be representative of a sizeable part of the stand in which it is located; and (3) it should not cross any obvious transition zones or boundaries in the vegetation.

This set of rules greatly limited the number of sites available, especially in Switzerland, where the forest was severely damaged by a heavy snow-fall early in this study. It is thought that the sample plots chosen represent a fairly random sample of the forests in both localities (Switzerland and Canada).

The samples (line intercepts, quadrats) were located at random, within the boundaries of each plot ( $10 \times 10$  m in Switzerland and  $50 \times 50$  ft in Canada).

Four methods were employed in measuring the vegetation:

#### (1) *The Braun-Blanquet method*

In each sample plot a complete list was made of all species present, with an ocular estimate of their cover and abundance (Appendices I and II).

#### (2) *The contiguous quadrat method*

Ten randomly distributed, 1-square-meter quadrats each divided into 16 equal squares with sides of 25 cm, were used. The percentage cover was estimated for four different sizes of quadrats; 160 quadrats of  $25 \times 25$  cm, 40 quadrats of  $50 \times 50$  cm, 10 quadrats of  $75 \times 75$  cm and 10 quadrats of  $100 \times 100$  cm.

#### (3) *The contiguous point-quadrat-line method*

This is the method developed and used by Kershaw and called by him, the line-interception method (KERSHAW 1958). The name used here was created to differentiate it from the line-interception method as devised originally by CANFIELD (1941).

A frame, consisting of two parallel sheets of plexiglass ( $24 \times 10$  cm) bolted together, approximately 8 cm apart, with a series of 20 holes, 1 cm apart, along either edge of the plexiglass, was used (KERSHAW 1958). By pivoting this frame around a pin through either end of the frame, it was possible to take contiguous readings of the vegetation along