varied between 75 and 95 years. The greater basal area on some sample plots are solely the result of a greater number of trees per unit area. The differences in the numbers of trees per unit area are thought to be the result of the action of a number of factors. All stands in the Candle Lake area originated after forest fires. The severity of the fires is an important factor determining the degree to which the original ground cover is modified, the degree to which the humus is burned, and the extent to which the roots of the original species were killed, etc. Another important factor is the availability of seed, which is governed by the distance to the seed source and the abundance of the seed (good or bad seed years). Even if all above factors are favorable, the establishment of seedlings is not ensured unless the weather cooperates with a series of moist growing-seasons after germination takes place. The differences between the densities of the stands, therefore, are primarily the result of differences in stand history and not so much the result of habitat differences or differences in the stages of development.

A large part of the variation of *Pleurozium schr.* is concentrated to the second principal axis. This second axis was found to be related only to the amount of "available moisture". It is, however, suspected that other factors of which no measurements were taken are also involved. The percentage cover of *Pleurozium schr.* increases with decreasing "available moisture" (Figs. 26 and 32).

The third principal axis, and also the third main axis, were found to be related to the "measured mean pH" of the humus layer. All the species mainly associated with these axes *(Linnaea borealis* var. *americana*, *Petasites palmatus*, *Cornus canadensis*, *Mertensia paniculata*, and to a lesser degree *Rubus pubescens*, *Fragaria virginiana*, *Mitella nuda*, and *Maianthemum canadense)* have their roots largely in this soil horizon. The pH and associated factors of this soil layer, then, are the most plausible factors in explaining the variation in distribution of these species. All the response curves along this axis had the same shape, with optima occurring between pH 4.5 and 5.5 (Fig. 27).

8. Conclusions

The purpose of organizing vegetation data is to symplify them in such a manner that a simple expression of the abundance, spacing, and other attributes of the plants emerges. Depending first on the spatial distribution of the different communities, this simplification can take two forms: an ordination and, if possible, a classification.

The foregoing study is primarily an example of the combination of two different techniques for organizing vegetation data: ordinating, and classify-

ing. A number of ordinating techniques were employed: Principal component analysis of the covariance matrix; Torgerson's method for analysing the D^2 matrix; and principal component analysis of the $(1 + D^2)^{-1}$ matrix.

The possibilities of classification were investigated by cluster analysis, based on an ordination of the sample plots, and by the differential species-group method.

Under theoretical considerations several requirements were advanced which should be satisfied by an efficient method for vegetation analysis (see chapter 4.4). The two methods for classifying and the three methods for ordinating vegetation samples will now be evaluated in the light of these requirements.

First, the ordinations will be considered separately from the cluster analysis, because theoretically the cluster analysis can be used with any of the ordinating methods. The differential species-group method is basically different from the cluster analysis and will be treated separately.

The principal component analysis of the covariance matrix and the D^2 ordination (Torgerson's method) were the most successful in ordering the vegetation samples in the simplest possible manner and account for the largest possible part of the variation within the samples. In the analysis of the Swiss data, the percentages of the variations accounted for by the first two principal axes of the covariance matrix, the first two main axes (D^2 ordination), and the first two principal axes ($(1 + D^2)^{-1}$ matrix) are 64.06, 88.17, and 14.71, respectively. In the analysis of the Canadian data these percentages are 80.00, 72.93, and 13.79, respectively.

Considering the labour involved in the construction of the main axes (D^2 ordination) and in the calculation of the percentages of the variation accounted for, the principal component analysis of the covariance matrix is preferable to the D^2 ordination. The principal component analysis of the $(1 + D^2)^{-1}$ matrix is unsatisfactory, in view of the low percentages of variation accounted for.

With regard to the second requirement, the principal axes of the covariance matrix are more closely related to the habitat features than either the D^2 ordination or the principal axes of the $(1 + D^2)^{-1}$ matrix. This is evident when the graphs of these relationships are compared. The points in the scattergrams are much more closely distributed around the fitted curves in graphs of the relationships among the principal axes of the covariance matrix and the habitat features (Figs. 16, 17, 28, up to and with 33) than in the graphs of the other relationships (Figs. 19, 20, 21, 22, 35, and 38). The correlation coefficients between the basal area of *Picea gl.* and the first principal axis of the covariance matrix, the first main axis, and the first principal axis of the $(1 + D^2)^{-1}$ matrix, are –.745, –.725, and –.592, respectively.

Requirement 3 is best satisfied by the D^2 ordination and the principal component analysis of the $(1 + D^2)^{-1}$ matrix, because both the cluster analysis and the two ordinating methods are based on the D^2 statistic. It is possible, however, using the Pythagorean theorem, to calculate the distances between the plots in the space described by the principal axes of the covariance matrix. These distances then, can be used in the cluster analysis, as were the D^2's, to determine if (and what) grouping can be recognized. Any one of the three methods, thus, easily satisfies the requirement of a common basis both for the cluster analysis and for the ordination. The use of the principal component analysis of the covariance matrix reduced computing time, which in most cases, however, is not a major consideration.

The requirement that the method should furnish a means of placing newly measured vegetation samples in a previously derived ordination or classification (4) can be satisfied in two different manners: by a quick provisional, or a slow, more accurate method. To be able to place a newly measured sample plot provisionally in an ordination or group, the distribution of some species should quantitatively be closely related to each of the axis of the ordination. This is a variation of the concept of characteristic species. Here, the quantities of the species instead of their presence are used to ordinate or classify vegetation samples. These species could conveniently be called "ordinator species". The principal component analysis of the covariance matrix fulfilled best the condition mentioned previously (see Figs. 24, 25, 26, and 27). Some of the relationships are not rectilinear. The coefficient of the eigenvector, thus, is not the best expression for the closeness of the relationship. A better statistic is the variance ratio. The variance ratio is the ratio between the mean square of the total variation due to the regression and the mean square of the residual variation. It is a measure of the goodness of fit of the regression line to the quantitative data. The goodness of fit of a number of curves can be compared directly, if the number of degrees of freedom is the same for all curves compared. The variance ratio calculated for the relationship between *Hylocomium spl.* and the first principal axis of the covariance matrix (Fig. 24) was 329.9. The variance ratio for the regression between *Pleurozium schr.* and the second principal axis, where the relationship is obviously not as close (Fig. 26), is 30.87. Both curves are highly significant (41 degrees of freedom, $P \leqq .001$).

The placing of newly measured vegetation plots in an ordination can more accurately be accomplished by multiplying the quantity of each species with the pertinent coefficient of the eigenvector and by summing the products. This will result in more precise coordinates for the sample plots.

Many ecologists and other workers (e.g. foresters) tend to feel uneasy as soon as the words "continuum" or "ordination" are mentioned. This is

mainly the result of unfamiliarity with the use that can be made of the results of an analysis based on this concept. The chief objections are the difficulty of mapping ordinated vegetation samples or of using them in management plans. This problem, however, is not always as serious as it appears to be. Even if it is impossible to classify vegetation samples, in the field it is usually quite easy to recognize stands which are rather homogeneous over extensive areas and which have sharp boundaries where they border on other stands. The stand then becomes the basic unit to be mapped and to be used in management plans. If the structure of the vegetation can be adequately described by three components (axes), each stand can be denoted by a set of three coordinates. These three coordinates describe its location in the ordination. This satisfies the fifth requirement.

In summary, the following can be suggested. Principal component analysis of the covariance matrix is superior in most of the aspects considered. The D^2 ordination developed by Torgerson ranks as the second best. The principal component analysis of the $(1+D^2)^{-1}$ matrix is unsatisfactory. It is possible, however, that other transformations of the D^2 matrices will result in a more satisfactory analysis.

Most of the foregoing considerations are also valid for the cluster analysis, because this is based on the ordinations. Since the principal component analysis of the covariance matrix results in an ordination of which the axes are most closely related to habitat features, it is to be expected that a cluster analysis based on this ordination would result in a grouping of the vegetation samples which is ecologically also most significant.

All the projections of the plots on the planes spanning the various axes indicated the same groupings, which were also supported by the cluster analysis. These groups were shown to be ecologically significantly different. Hence, no attempt was made to perform a cluster analysis on the distances in the space described by the principal components of the covariance matrix.

Both the grouping of sample plots according to the differential species-group and the cluster analysis satisfy, as most classifications do, the condition that the ordering of the vegetation samples should be simple. It is very difficult, however, to determine what part of the total variation is accounted for by the grouping according to the differential species-groups. In the grouping according to cluster analysis the variation accounted for is the same as that accounted for by the principal axes.

The cluster analysis, in the case of the Swiss data, resulted in five groups which are differentiated along one or more principal axes. A relationship among two axes and soil pH and light conditions was established. This indicates that the groups were differentiated by more than one habitat factor.

The differential species-group method resulted in three groups of sample plots, which were significantly differentiated with regard to soil pH but not with regard to light conditions.

The condition that it should be possible to place a newly measured sample plot into a previously derived classification (4) is best met by the differential species-group method. No accurate measurements of species-cover or computations are necessary. The presence or absence of the species belonging to these species-groups determines the vegetation-type in which the sample plot should be classed.

The decision to group sample plots together is, in the case of cluster analysis, based on the quantities of the species belonging to several groups, not just their presence or absence as in the differential species-group method. Within each group, the species which have a high coefficient for the eigenvectors representing that group have strong positive or negative quantitative relationships. The species belonging to such a group represented by one axis, respond highly to the level of the habitat factor (or factors) to which the axis is related. Species belonging to all groups may be present on a sample plot in different quantities, thus facilitating the quantitative differentiation from other sample plots along several habitat factor gradients. The cluster analysis thus results in a finer and ecologically more sensitive division of the vegetation than is possible by the differential species-group method. Also finer-grained classification systems, as result from cluster analysis, are less likely to have sample plots classified in the "remainder class".

As prooved since long, the vegetation units established by means of the differential species-group method are easy to map. It also satisfies the requirement of simplicity quite well and is least time consuming. Therefore, the classification according to the differential species-group method should be preferred for initially *describing and mapping* the vegetation.

The ordinating methods besides forming the basis for cluster analysis, should preferably be used to elucidate relationships within vegetation units (community-types), because the requirement of linear relationships is closest met in such a case. The data of each unit are again analysed separately. In this study, the number of Swiss sample plots in each unit was too small to warrant such a procedure. The Canadian sample plots, however, can, for practical purposes, be considered as representing one vegetation type, and, as such, the ordination of these plots can be considered an example of such an ordination within a vegetation-type.

The combination of ordination and classification into one method has several advantages:

(1) It offers an *objective* method for classifying vegetation samples.

(2) If classification is not possible, it accords the investigator an alternative in the ordination; and

(3) if classification is possible, one often would like to know if the levels of the factors in which one is interested are significantly different in the community-types recognized. This could be investigated by a variance analysis or by a "t" test. If the relationships among the factors and the axes are known, however, it can easily be shown that, in most cases, only those habitat features, that show a significant relationship with the axes, have significantly different means for the different community-types. This does not mean that they have to be significantly different. This depends on the relative position of the clusters in relation to the axes.

It was hypothesized that the correlations or covariances between the quantitative measures of the different species were not due to chance, but were reflections of the reaction of the species to their environment, including the interactions between the species. The relationships which were found to exist between the principal axes and certain habitat factors are an indication of the correctness of this concept.

The fact that the ordinations of the Canadian sample plots are not related either to the height-growth or to the nitrogen content of the white spruce foliage attracts attention. To obtain an ordination which also would be related to these factors, certain soil factors, which were not measured in this study, should be included in the analysis, or better yet they should be analyzed separately for their relationships with the height-growth and nitrogen content of the foliage.

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