(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 (10×10 m in Switzerland and 50×50 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 25×25 cm, 40 quadrats of 50×50 cm, 10 quadrats of 75×75 cm and 10 quadrats of 100×100 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 (24×10 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

straight lines. Adjacent readings were grouped into units of 5 cm. The length of the lines was 6 m, for a total of 60,000 points per plot.

(4) The line-interception method (CANFIELD 1941)

A tape-measure was stretched tight between two pins, 6 meters apart. For each species, the beginning and the end where the line crossed the species, were recorded to the nearest mm. The data were tape-recorded and later reconstructed on paper. The line was divided into contiguous pieces, 5 cm long. Then, the percentage cover for each species over each 5 cm of the transect was determined.

5.1.2 Variance analysis

To determine that size of quadrat, or length of line (point-quadrat-line or line-intercept), that was most efficient in decreasing the variance, the variance was calculated for each size of quadrat (respectively 25×25 cm, 50×50 cm, 75×75 cm and 100×100 cm) and for different lengths of line-intercept (respectively 5, 10, 20, 40, 80, 160, 300, and 600 cm long). The variance was then plotted against quadrat size or length of line.

This variance analysis technique also makes it possible to check whether the species form a small scale non-random pattern (GREIG-SMITH 1952), because the variance rises to a peak in the graph at a sampling-unit size equivalent to the size of the pattern.

In some cases, the frequency distributions of the cover percentages were plotted for different sizes of line-intercept to show the increased normality of distribution with increased length of line-intercept (Fig. 1).

By plotting the increase in number of species encountered through increases in the number of quadrats or lines, the efficiency of these methods for producing estimates of the cover of as many species as possible was estimated.

5.1.3 Relationship between distribution of light levels and plant species, within sample plots

For each plot, the levels of light as measured by two different methods along five line-intercepts was plotted against the percentage cover of the more abundant species as measured on contiguous 10 cm sections along these lines.

5.1.4 Classification of sample plots according to the Zürich-Montpellier method

The species and sample plots were arranged and grouped in such a manner that groups of species (differential species-groups) which would occur only in a certain group of sample plots (see Appendices I and II) became evident. The sample plots were classified according to the presence or absence of the species belonging to these differential species-groups.

5.1.5 Principal component analysis of the covariance matrices

For reasons later explained, only the line-intercept data were used for computing the principal components and the D^2's.

The actual analysis was performed by IBM 7090. The program was developed and written by Dr. Ihm of the Euratom Research Centre at Ispra, Italy (1964).

5.1.6 Computation of the D^2 matrices

The D^2's (Mahalanobis' generalized distances) between the plots and their significance levels, were computed by IBM 7090. The program was developed and written by Dr. P. Ihm.

5.1.7 Analysis of the D^2 matrices

A two or three dimensional ordination was constructed from the D^2 data according to Torgerson's method. The correlation coefficients and their significance levels were calculated among the distances in the two dimensional projections and the D^2's. The square power of these correlation coefficients indicate the percentages of the total variation accounted for by the ordinations.

5.1.8 Principal component analysis of the transformed D^2 matrices

As mentioned before a D^2 matrix can not conveniently be analysed by principal component analysis. Two transformations were performed:

$$R_1 = (1 + D^2)^{-1}; \text{ and } R_2 = e^{-D^2},$$

with the help of a G-20 computer.

The transformed D^2 data were analysed by the Statistical Research Service of the Canada Department of Forestry in Ottawa, using a G-20 computer.

As stated before, the method is explained in appendix V and will not be treated here.

5.1.9 Cluster analysis

The projections of the points on the planes spanning the three principal axes were examined for indications of clustering. The projections on the planes spanning the three main axes of the constellation of points described by the D^2 matrix (according to Torgerson) were examined likewise.

The D^2 matrix was analysed for clustering by the method due to Tocher.

5.2 *Habitat features*

Different features were measured and sometimes different methods were followed for the Swiss *Abies* and Canadian *Picea* forests.

5.2.1 Swiss data

(1) The soil pH was determined on 50 random samples within each sample plot, according to the method described by DOUGHTY (1941).

(2) The light conditions in each plot were determined on sunny days, along 5 random, 6-meter lines (identical in location to the line-intercepts), with a method developed by the author during his stay at the Geobotanical Institute at Zürich (method 1, VAN GROENEWOUD 1963) and also with a portable electric light meter (Lange), on completely overcast days (method 2).

5.2.2 Canadian data

(1) Basal area, defined as the sum of the cross-section areas of all boles at breast height (4 ½ feet), is expressed in terms of square feet per acre. The trees on all plots were tallied for diameter and the data converted to area of cross-section.

(2) Height-growth curves were constructed for four of five dominant white spruce trees on each sample plot. The trees were felled and sectioned at 5-ft intervals; the growth rings were counted at each interval, and from these data the growth curves were constructed. The height-growth (ft/year) during the "intermediate" stage (BAKER 1950) was determined and this index was used as an index of site quality.

(3) The soil profiles on all sample plots were described in detail as to depth and thickness of all soil horizons, distribution of feeder roots, estimate of soil texture and structure, and soil colors on air-dry samples (Munsel color charts).

(4) The permanent wilting point (P.W.P.) was determined with a pressure membrane apparatus on 4 samples of the A_2 horizon of each sample plot. The results are expressed on a per cent dry-weight basis.

(5) The field capacity (F.C.) was determined as follows: Five small isolation plots were established at random within each sample plot (roots were cut, top of vegetation removed). Each isolation plot was drenched and covered with plastic sheeting to reduce evaporation. The soil was allowed to drain for 4 days, after which two samples were taken from the A_2 horizon of each isolation plot. The results are expressed on a per cent dry-weight basis.

(6) "Available moisture" was determined by calculating the difference between P.W.P. and F.C.

(7) The pH of the soil was determined in the field or in the field laboratory within a few hours after sampling, using a Beckman pH meter (Beckman Instruments, Inc., 2500 Harbor Blvd., Fullerton, California) with a combination glass electrode. The soil was prepared as a soil paste according to DOUGHTY (1941). The "measured mean" and the range of pH on each sample plot were determined (VAN GROENEWOUD 1961).

(8) Samples of foliage were taken in midwinter and always from the tops of the trees, to minimize the effects of seasonal fluctuation and of position on the tree. The tree tops were shot down with a .22 caliber rifle with telescopic sight. The foliage was kept at –18°C until it could be further processed. The spruce needles were dried at 60°C. After drying, scales and other contaminations were removed by hand. Dust adhering to the foliage was removed with an air-jet of 60 p.s.i. The samples were ground in a Wiley mill and stored at –18°C until the analysis could be performed. The nitrogen content was determined by the micro-Kjeldahl method. The results were corrected for moisture content of the samples at the time of analysis. Ten samples were analysed from each of the 43 plots. This number was considered necessary, because a preliminary study revealed considerable variation in foliage composition within each plot.

5.3 *Interpretation*

The habitat features were all tested for their relationship with the principal axes (covariance matrix), with the main axes of the constellation of points described by the D^2 matrix, and with the principal axes of the transformed D^2 matrices.

The levels of the habitat feature to be tested, were plotted against the corresponding projection of each plot on each axis. If a relationship was evident, a line or curve was fitted to the points. Where a straight line relationship was found, a correlation coefficient was calculated.

When groups of points could be recognized in the ordination, the differences among the mean levels of the habitat features in these groups were tested by a modified "t" test only for those features that had shown a relationship with the principal or main axes.

The differences among the mean levels of the habitat features in the groups of sample plots, as distinguished by the differential species-group method, were tested by "t" tests. To obtain a measure of the separation of the ranges occupied by these groups along the various gradients, the sum of the standard deviations were compared with the differences among the means.

6. Results

Only a relatively small number of the several hundreds of graphs prepared to test all possible relationships is presented. The number of figures has been limited by applying the following rules:

(a) only statistically significant relationships are shown;