

Zeitschrift: Berichte des Geobotanischen Institutes der Eidg. Techn. Hochschule, Stiftung Rübel

Herausgeber: Geobotanisches Institut der Eidg. Techn. Hochschule, Stiftung Rübel

Band: 36 (1964)

Artikel: Ordination and classification of Swiss and Canadian coniferous forests by various biometric and other methods

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Kapitel: 7: Discussion

DOI: <https://doi.org/10.5169/seals-377646>

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6.3.9 Clustering of sample plots

Neither the projection of the points representing plots on the planes spanning the principal axes, nor the projection on the planes spanning the main axes of the constellation described by the D^2 matrix, showed any tendency of clustering.

Practically all D^2 's were significant ($P \leq .05$). A group of thirteen sample plots, all with a high cover percentage for *Picea glauca* and *Hylocomium splendens*, had very few significant D^2 's among them. Because the significance of the D^2 's, however, is greatly dependant on the number and size of the samples, it is not a satisfactory criterion for grouping sample plots.

The D^2 matrix was also analysed by the method developed by Tocher. This analysis showed that no clustering of the points occurred.

7. Discussion

A comparison of the data obtained by three different methods of sampling indicates that there is no single procedure which is superior in all respects. An intensive investigation of this problem should involve a time-study and include different types of vegetation. This was outside the scope and interest of this study.

Of the three methods tested, the quadrat method was the quickest, but it was not generally superior either in the relative number of species sampled or in minimizing the variance. In fact, increasing the size of the sampling quadrat did not markedly decrease the variance. This is probably due to an increased error in the estimates of the cover percentages with increased size of sampling unit.

The point-quadrat-line method as used by Kershaw, was quite as efficient in the relative number of species sampled and it was much more efficient in minimizing the variance than the quadrat method. This method was, however, more time consuming than the line-interception method, due to the particular type of distribution of the species (mostly mosses).

The line-interception method was equally as efficient in the relative number of species sampled and in minimizing the variance as the point-quadrat-line method. The agreement between the data by the last two methods was very close ($r = .9994$, $P = .001$).

Summarizing, it can be stated that, in the particular vegetation types investigated, considering the accuracy of the estimates required for this study, the line-interception method proved to be the most efficient way of sampling.

Greig-Smith developed a method of continuous sampling, later improved by Kershaw, to study non-random pattern in the distribution of single species. The theory is that if species are not distributed at random, this indicates the heterogeneity of the habitat with respect to one or several factors, or groups of correlated factors, which determine the occurrence and performance of the species. This is analogous to classification, but on a small scale.

The possibility still remains that the species distribution is determined by one or several factors, without showing a non-random pattern, if the different levels of these factors are also distributed at random. Other methods should then be used.

In this study, non-random patterns were not evident within the area of the sample plots. It was suspected, however, that light played an important role in determining the distribution of the species. This aspect was studied in the Swiss forests. Only in very few cases could a relationship be demonstrated, e.g. with *Sphagnum quinquefarium* (Fig.12). It is, however, suspected that other factors of which no measurements were taken are also involved.

Two methods were used to measure the light conditions along the same line-interceptions. The first method measured the integrated effect of the light over a 24-hour period during sunny weather; the second method made use of a photoelectric measuring device on days with a continuous cloud cover. Comparisons show completely different distributions of light on the forest floor as measured under these conditions (Fig.13). The only exceptions occurred when the canopy was very dense, with only a few openings. Under these conditions, the distributions of light levels show closely similar patterns (Fig.12). The distribution of different levels of precipitation, however, would also show a closely similar pattern. The question remains regarding which of these factors is the most effective in determining the distribution of *Sphagnum girgensohnii*, because no measurements of soil moisture availability were made.

The grouping of the forest vegetation sampled in Switzerland, which is evident in the projections of the points representing sample plots on the planes spanning the principal axes of the covariance matrix and on the main axes (D^2 matrix), is further objectively demonstrated by the cluster analysis due to Tocher (Appendix III). In addition, it is shown that among groups, significant differences exist in the levels of light received at the forest floor. Four of the five groups also have significantly different soil pH's.

The grouping of the Swiss sample plots, according to the Braun-Blanquet method of differential species-groups, resulted in groups of sample plots which had significant differences in average soil pH's, but with no significant

differences in the average light levels received. The grouping of the sample plots, according to the Zürich-Montpellier method, runs to some extent parallel to the grouping due to the cluster analysis. The separation of the groups along the pH-gradient is a little better in the grouping due to cluster analysis than in the Zürich-Montpellier grouping.

In the grouping due to the cluster analysis, there are significant as well as non-significant differences among the groups. The differences in the mean light levels, however, are practically all significant. In other words, some of the groups were not differentiated from others with respect to soil pH, but were differentiated from these groups by significant differences in light levels. Because the grouping of the various sample plots in the cluster analysis is directly related to the position of each sample plot in the ordination, it is more interesting to discuss this grouping after the discussion of the ecological meaning of the ordination.

Although classification or grouping of sample plots in most cases is adequate and convenient as far as simplification of the description of the vegetation and habitat conditions is concerned, it is not so satisfactory if the object of study is the underlying pattern of quantitative relationships among species, and between species and habitat factors. As far as information on the ecological behaviour of the species and of the whole vegetation is concerned, the ordinations are far more revealing than the groupings.

Groups of sample plots may have significantly different means for certain features as a result of a particular spatial distribution of these features, without having any direct relationship with the distribution of the vegetation. This will be later illustrated on the Canadian data. The possibility that the wrong conclusions are drawn, can be obviated if significant relationships are sought first between the levels of the features and the ordinations. Only the means of those features that show a relationship with the principal or main axes have to be tested for significant differences. It depends on the relative position of the groups involved, in relation to the principal or main axes, whether a significant difference will be found.

The results of the three ordinating methods are in good agreement as far as the relationships with the habitat features are concerned. The P.C.A. of the covariance matrix is, however, generally the most satisfactory method (see later discussion). Consequently, only the result of this method will be discussed in relation to the habitat features.

Since the first principal axis is related to light conditions and the third axis to soil pH (Swiss data), it is interesting to consider the extent to which each species contributes to the various principal axes.

The species that have high coefficients contributing to the eigenvector of

the first eigenvalue (first principal axis, light conditions and related factors), *Polytrichum formosum*, *Abies alba*, and *Picea abies*, are also important in the second principal axis. The second axis, however, is not related to the two habitat factors measured. Because no other measures of the habitat were taken, it was impossible to establish the ecological meaning of this axis.

It was observed that *Polytrichum f.* forms large carpets under small openings in the *Abies a.* canopy, where there is an increase in light. This agrees well with the relationships as indicated by the coefficients of the pertinent eigenvector. *Polytrichum f.* increases with decreasing *Abies a.* and increasing light.

The relationship between *Polytrichum f.* and *Picea a.* also agrees well with the observations. As *Picea a.* increases in relative importance in the stands, the canopy tends to be more open (note that *Abies a.* has a positive and *Picea a.* has a negative coefficient for the pertinent eigenvector).

The main species that contribute to the third principal axis are: *Oxalis acetosella*, *Eurhynchium striatum*, *Sphagnum quinquefarium*, *Bazzania trilobata*, and *Vaccinium myrtillus*. *Oxalis a.* and *Eurhynchium s.* tend to increase in importance with increasing soil pH. *Sphagnum q.*, *Bazzania t.* and *Vaccinium m.* increase in importance with decreasing soil pH (Fig. 39).

It is evident that the coefficient for *Sphagnum q.* in the first eigenvector is positive and rather small, indicating a small positive correlation between the quantitative measure of *Sphagnum q.* and *Abies a.* on these sample plots. This seems to be in direct contradiction to the results of the study of the relationships between light and species along the line-intercepts. The reason for this apparent contradiction can be found in the special ecological niche that *Sphagnum q.* occupies in these forest stands. In dense forest, it only occurs under small openings in the canopy. In a study using measuring units larger in size than these openings, this special relationship is obscured. The above shows the importance of the study of distinct ecological niches within the general habitat, in relation to the occurrence of certain species.

Bazzania trilobata also has a positive coefficient of the first eigenvector, likewise indicating a positive correlation between the occurrence of *Bazzania t.* and *Abies a.* In contrast to *Sphagnum q.*, however, this reflects a true relationship.

After foregoing observations on the relationships among the principal axes, habitat factors, and species occurrence, it is conducive to a better understanding of the significance of the grouping of the sample plots, resulting from the cluster analysis, to consider these groups in the light of the ecological and sociological affinities between the plots, expressed by the relative position of each sample plot in the ordination. An inspection of the ordination (Fig. 14)

shows that each cluster is differentiated along one or more axes. Clusters which are more or less distinct along all three axes, e.g. cluster I and V, occupy different ranges along the light, soil pH gradients (and possibly a third gradient), because these gradients are correlated to a certain degree with the principal axes. Besides being ecologically differentiated, these clusters are also distinct with regard to the level of occurrence of the species associated with these principal axes, e.g. clusters I and V respectively, have relative high and low cover-percentages for *Abies a.* (65 and 20%) and low and high cover-percentages for *Polytrichum f.* (3 and 63%). Both clusters have relative high cover-percentages for *Oxalis a.* (app. 15%).

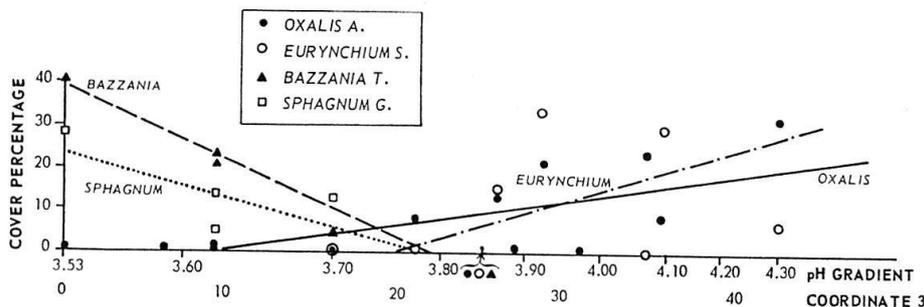


Fig. 39. Levels of occurrence (percentage cover) of *Oxalis acetosella*, *Eurhynchium striatum*, *Bazzania trilobata* and *Sphagnum quinquefarium* along the pH gradient (coordinate 3, covariance matrix, Swiss data).

Other clusters are clearly differentiated only along one axis, e.g. clusters I and III along axis 3. These two clusters occupy different ranges along the soil pH gradient (correlated with the 3rd axis), but are not significantly different with regard to light conditions. Vegetationally, these clusters are differentiated by having high and low cover-percentages for the following species: *Oxalis a.* (30 and 0%), *Eurhynchium s.* (7 and 0%); or low and high cover-percentages for *Sphagnum q.* (0 and 20%), and *Bazzania t.* (0 to 30%).

If the correlation between axis and habitat factor is not too close the relationship between the relative positions of the clusters with regard to the axis, and the level of the habitat factor, as represented by their position along the axis, breaks down. An example of this is clusters IV and V, which occupy the same range along axis 1, but which have significantly different mean levels of light, 47.89 and 15.02 kilo-Lux-hours per day, respectively.

The eigenvalues for the fourth and fifth axes are of such magnitude, that they have no practical importance.

Both the projections of the points, representing the Canadian sample plots, on the planes spanning the principal axes and the projections of the planes spanning the main axes of the constellation of points, as described by

the D^2 matrix, gave no indication of clustering. Attempts to find local concentrations of points according to Tocher's method, also failed. The conclusion must be drawn, then, that grouping according to these methods is not possible. It was found, however, that it was possible to divide the vegetation samples into three units on the basis of presence or absence of species belonging to certain groups (the differential species-group method).

A statistical analysis of the mean levels of the habitat and other features in these units revealed that division into these three groups was of limited ecological significance. Of the fifteen factors measured, only units II and III are significantly different, with regard to the field capacity of the mineral soil (15.20% and 15.36% respectively). Units I and III are significantly different with regard to the "available moisture" of the mineral soil (11.52% and 13.93% respectively) and also with regard to the height-growth of the spruce trees (1.075 and 1.182 ft/yr respectively). The significant differences between units I and III with regard both to "available moisture" and to height-growth suggests a significant relationship between the habitat and the biotic factor. If the data were taken only from the sample plots belonging to units I and III, the correlation was .43 ($P = .05$). When the data of unit II were included, however, the correlation decreased to .20 which was not statistically significant. The implication is that another habitat factor (or set of factors), about equal in importance to the growth of white spruce as the "available moisture, reaches such levels (both high and low) in the sample plots belonging to unit II, that an equally high and low level of growth is reached in this type as under the influence of the high or low levels of "moisture availability" in the sample plots of units I and III. The relationship between height-growth and "available moisture", is, then, not very stringent.

The interpretation of the ecological meaning of the principal and main axes is thought to be as follows.

Both *Picea glauca* and *Hylocomium splendens* have high coefficients, contributing to the eigenvector corresponding to the first eigenvalue. In other words, their variation is concentrated to the first principal axis. Their quantitative relationship with this axis is shown in Figs. 24 and 25. With increasing cover of *Picea g.*, *Hylocomium spl.* also increases.

The precipitation in the area investigated, is low; approximately 6 inches (15 cm) during the growing season. With increasing density of *Picea g.*, the interception by the canopy increases in proportion. Other workers have found up to 45% interception (NOIRFALISE 1959, DELFS 1954, LAW 1956). Besides decreasing the amount of precipitation reaching the forest floor, *Picea g.* with its superficial root system is a strong competitor for moisture in

the top four inches (10 cm) of the soil. At the same time, the increasing density of the canopy results in decreasing quantities of light reaching the forest floor.

According to STÅLFELT (1937), *Hylocomium spl.* is a species which can withstand complete air drying without being killed. This explains the increasing cover of *Hylocomium spl.* under these conditions, which are too severe for other species to survive.

Pleurozium schreberi also can withstand dry conditions, but needs more light to survive. This explains why *Pleurozium schr.* increases up to a certain level with increase in density of *Picea g.*, but after reaching this peak drops off sharply (Fig. 25).

As expected, the basal area of *Picea g.* (as it is related to the cover-percentage) is strongly associated with the first principal axis and the first main axis, with correlation coefficients of $-.745$ and $-.725$, respectively (Figs. 27 and 35). P is in both cases less than $.001$. The basal area was primarily taken as an index of the competition between the trees. STENEKER and JARVIS (1963) found a strong correlation ($r = .83$) between the ten-year radial increment and the basal area of *Picea g.* within a radius of 15 feet (app. 4.5 m). It can be deduced that in the communities, typified by a high cover-percentage of *Hylocomium spl.*, competition is extremely high. Diameter-growth slows down, but height-growth and the nitrogen content of the foliage do not seem to be affected.

Also interesting is the relationships of the "measured mean" pH of the fermentation layer, the maximum pH of the mineral soil, and the humus layer with the first principal axis (or first main axis). As the density of *Picea g.* increases (Fig. 25) and that of *Populus tremuloides* decreases (Fig. 25), the "measured mean pH" of the fermentation layer becomes gradually lower (Fig. 31). This is in agreement with the generally accepted concept that the pH of the organic layer is lower under coniferous than under deciduous trees (AALTONEN 1940, OVERTON 1953). It is noticeable, however, that the maximum pH's of the humus layer and the top of the mineral soil show the opposite tendency. The maximum pH's become higher (Figs. 29 and 30) with increases in the density of *Picea g.* and decreases in *Populus trem.* (Fig. 25). The author believes that this can be attributed to the lesser degree of leaching which occurs under dense spruce stands and the higher degree of litter decomposition under mixed-wood stands.

The first principal axis (or main axis) could easily be mistaken to represent a developmental gradient, for it is strongly correlated with the basal area of the spruce trees which, up to a point, tends to increase with age. There is, however, very little difference in age of the trees in the different samples; all

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-