(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;

(b) further, only those relationships are shown that convey information not already contained in other graphs, unless they are used to prove a certain point, such as showing the differences in the results of relationships among the various methods.

6.1 *Sampling and small scale distribution*

6.1.1 Comparison of vegetation sampling methods

Several factors have to be considered in judging the relative merits of different sampling methods.

The vegetation data collected by the line-interception method were practically identical to those taken by the point-quadrat-line method. The correlation coefficient was .9994. To facilitate the presentation, the results of both methods were regarded as being identical.

(1) The first factor to be considered is the accuracy of the estimation of the mean cover per plot for each species.

The variation is dependent on the dimensions of each sampling unit (length of line-intercept, area of sampling quadrat), the spatial distribution of the species, and the number of samples. The variance was calculated for different sizes of sampling unit and plotted for both line-intercepts and quadrats. Some of the results are shown in Fig.8 and 9.
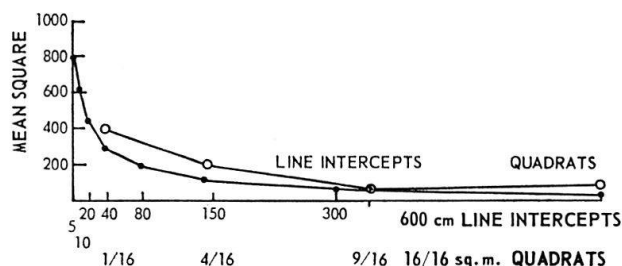

Fig. 8. Mean square/length of line-intercepts and mean square/quadrat size (*Oxalis acetosella*; plot 1, Ziegelwald, Roggwil).
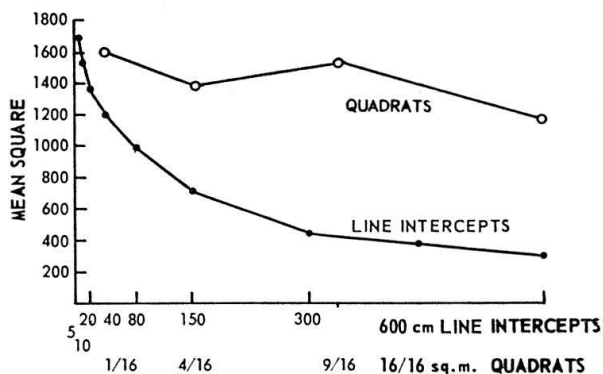

Fig. 9. Mean square/length of line-intercepts and mean square/quadratsize (*Polytrichum formosum*, Plot 4, Ziegelwald, Roggwil).

In general, the line-intercepts are more efficient in decreasing the variance with increasing size of sampling unit than the quadrats. This is probably due to the increased error in estimating the cover of the species with larger quadrats, opposed to the constant error by the line-interception method. For the same reason, the graphs of variance plotted against sample-unit size of the quadrat method also showed more irregularities than those of the line-interception method. The graphs of the line-intercept variance data were very regular.

These graphs also served to study the pattern of distribution of the species on the sample plots (see next paragraph)

(2) Another factor is the efficiency of the different sampling units in estimating the cover percentage of a high percentage of the total number of species present on the plot.

The results varied with the distribution of the species on the different plots. On some, the quadrat method was more effective; on others, the line-intercept (Figs. 10 and 11).

The overall assessment indicates that the line-interception method has the most advantages of the three methods.

The line-interception and the point-quadrat-line method have the added advantage that the vegetative cover can be rather easily related to habitat factors as measured along the lines.

Fig. 10. Increase in number of species sampled, with increase in the number of sampling units (line-intercepts and quadrats, plot 4, Ziegelwald, Roggwil).
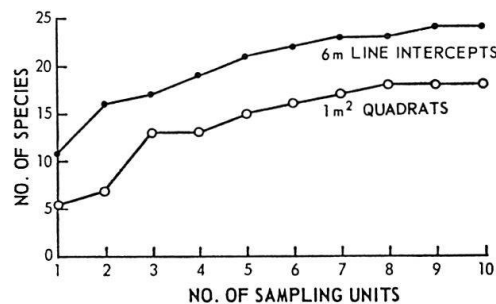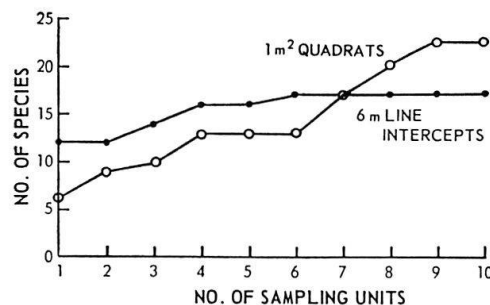

Fig. 11. Increase in number of species sampled, with increase in the number of sampling units (line-intercepts and quadrats, Plot 3, Ziegelwald, Roggwil).

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In this study, only the line-intercept data was analysed using the methods mentioned before.

6.1.2 Small scale non-random pattern within sample plots

Seventy variance analysis graphs were prepared, one of which (*Polytrichum formosum*, plot 2, Roggwil) showed a peak at a length of 40 cm line-intercept. This pattern did not interfere with the planned analysis and was too unimportant to induce further investigation. All other graphs showed decreasing
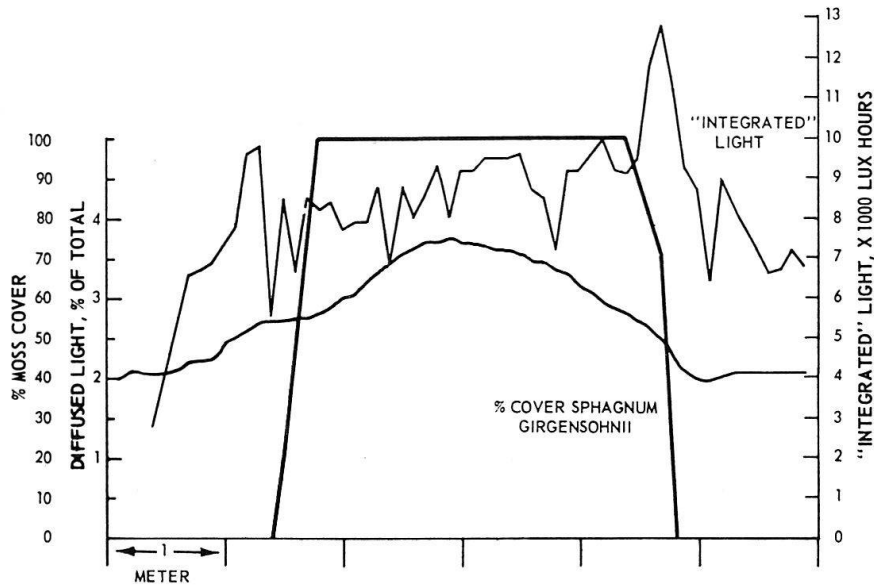

Fig. 12. Distribution of "integrated" and diffused light in relation to percentage cover of *Sphagnum quinquefarium* (not *girgensohnii*) along line-intercept (plot 10, line 3, Murgenthal).

variance with increasing lengths of line-intercepts, with an almost constant variance around a length of 600 cm (Figs. 8 and 9). Further increase of length of line intercepts would have been useless in this study. Based on this evidence, it must be assumed that, for the species investigated, *small scale non-random patterns were not present within these sample plots.*

6.1.3 Distribution of the vegetation along line-intercepts in relation to light.

The cover percentage of several species were plotted, together with light conditions along several line-intercepts of each plot. The data were collected in Swiss forests. The following results were noted:

(1) Only in dense forest did the measurements of the light conditions along the lines coincide (Fig. 12);

(2) In more open forest, the light as measured by the two methods shows an entirely different distribution pattern (Fig. 13);

(3) Only where the light, measured by the two methods, had the same

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distribution, was this distribution related to the distribution of the vegetation, in particular with *Sphagnum quinguefarium* (Fig. 12);

(4) A total of 50 light and vegetation graphs were plotted but the patterns coincided only in the case of dense forest.

At this point, results of the Swiss data will be presented first, to be followed by the results of the Canadian data. Both were subjected to *identical* procedures.
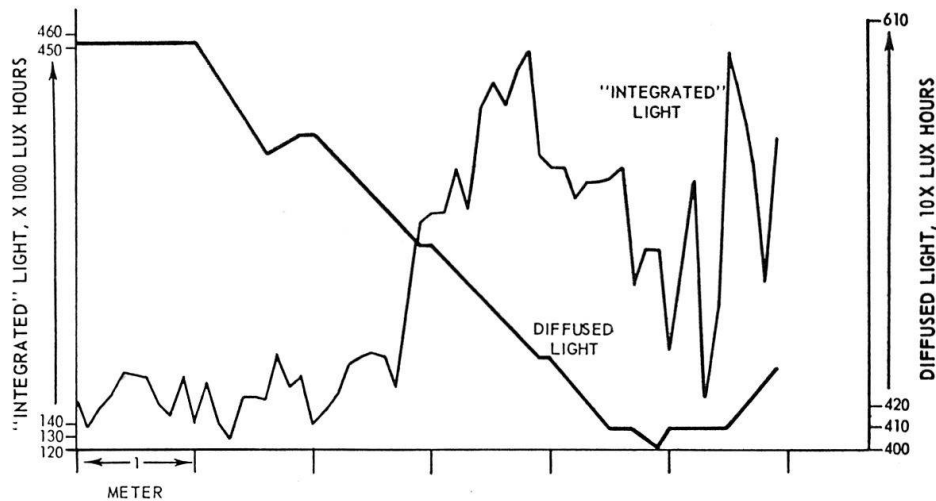

Fig. 13. Distribution of "integrated" and diffused light along line intercept (plot 12, line 5, Unterwald, Roggwil).

6.2 Swiss sample plots

6.2.1 Classification of sample plots (Zürich-Montpellier method)

Five groups of differential species were distinguished (Appendix I).

Group A comprises species which are present on all plots: *Vaccinium myrtillus*, the seedlings of *Abies alba* and *Picea abies*, *Hylocomium splendens*, *Rhytidiadelphus triquetrus*, *Polytrichum formosum* and *Thuidium tamariscifolium*.

Group B contains species which have fairly wide ecological amplitudes but which are particularly suited to delimit mull from mor soils (ELLENBERG 1963, p. 86). To this group belong the herbs; *Anemone nemorosa*, *Fragaria vesca*, *Hedera helix*, *Lysimachia nemorum*, *Viola silvatica*, *Galium rotundifolium*, and the mosses: *Catharinea undulata*, *Mnium undulatum* and *Mnium affine*. The species of this group are present on sample plots no. 1, 2, 3, 6, and 12 (Vegetation unit I) and are absent (2 exceptions) in the other plots.

Group C comprises species which obviously have ecological requirements close to those of group B, but are differentiated by a somewhat wider amplitude. The species of group C are: *Athyrium filix-femina*, *Dryopteris austriaca*, *Luzula pilosa*, *Maianthemum bifolium*, *Oxalis acetosella*, *Rubus* spec., and *Eurhynchium striatum*.

Group D embraces species which flourish on moderately dry to moderately moist sols with a lower soil pH than foregoing groups. The species of this group have ecological amplitudes, which partly overlap those of the species of group C, but which almost completely differentiate this group from group B. The species of this group are: *Pleurozium schreberi, Rhytidiadelphus loreus, Dicranum scoparium, Hypnum cupressiforme,* and *Plagiothecium undulatum.*

Group E comprises species which have their optima on moderately moist to moist, and very acid soils. The species belonging to this group are: *Bazzania trilobata* and *Sphagnum quinquefarium.* These species occurred only in sample plots no. 4, 5, 8, 9, and 10 (Vegetation unit III).

Group C and D help differentiate a group of sample plots, containing no. 7, 11, 13, 14, and 15, (Vegetation unit II), which is intermediate between the plots differentiated, respectively, by the *Anemone nemorosa* and the *Bazzania trilobata* groups.

6.2.2 Habitat factors in relation to classification of sample plots

The groups of sample plots established in foregoing paragraph received the following average amounts of light with their respective standard deviations (all expressed in kilo-Lux-hours per day): 14.72 ± 7.35, 19.22 ± 16.12 and 15.56 ± 6.72. The differences among these average levels are not statistically significant.

The average soil pH of these groups of sample plots, with their standard deviations are $4.04 \pm .38$, $3.83 \pm .29$, and $3.61 \pm .22$, respectively. The differences among the means are all statistically significant. If, however, the ranges along the pH gradient occupied by these Vegetation units are considered, it is obvious that only the pH ranges of unit I and III are separated to some extent; the differences between the means is .43 and the sum of the standard deviations is .60.

6.2.3 Principal component analysis of the covariance matrix

The principal component analysis resulted in principal axes with the following eigenvalues:

trace of matrix = sum of all eigenvalues = 31875.0

Axes Eigenvalues

I 12402.0 accounting for 38.91 % ($= 12402.0 / 31875.0 \times 100$) of the total variation.

II 8016.5 accounting for 25.15 % of the total variation.

III 3833.3 accounting for 12.03 % of the total variation.

IV 2335.0 accounting for 7.33 % of the total variation.

V 1798.2 accounting for 5.64 % of the total variation.

The first two axes account for 64.06%, the first three axes for 76.09, and the first five axes for 89.06% of the total variation.

The 38 coefficients of the eigenvectors are listed in table 1. The coefficients which contribute most are in italics.

It is noteworthy that the variance of many species can only be satisfactorily described by more than one principal component, e.g. *Oxalis acetosella* by

Table 1. Eigenvalues and eigenvectors of the Swiss covariance matrix.

	I	II	III	IV	V
Eigenvalues	12402.	8016.5	3833.4	2335.0	1798.2
Species			Eigenvectors		
1. *Oxalis acetosella*	−.02317	−*.17303*	*.43073*	*.44055*	*.20080*
2. *Carex brizoides*	−.00782	−.00447	.01609	.02238	.02894
3. *Rubus* spec.	−.00543	−.00143	.02031	.03411	.02734
4. *Polytrichum formosum*	−*.56862*	−*.74735*	−.06078	−.15409	−.15084
5. *Thuidium tamariscifolium*	.02274	.03175	.05320	−*.49471*	*.30432*
6. *Hylocomium splendens*	−.02362	.10902	−.13904	−.13432	−.10456
7. *Rhytidiadelphus triquetrus*	.01274	.01593	−.04597	.07050	.03977
8. *Abies alba* (seedling)	−.04874	.02277	−.04145	.03446	.03192
9. *Luzula luzuloides*	−.00270	−.00275	.00078	.00139	.00041
10. *Maianthemum bifolium*	−.01351	.00184	−.00046	.00083	.01423
11. *Vaccinium myrtillus*	−.11249	.16698	−*.27644*	*.26820*	.04920
12. *Hypnum cupressiforme*	−.00965	.03602	−.04853	−.01272	.02898
13. *Plagiochila asplenioides*	−.02236	−.00742	*.20060*	*.20261*	*.26078*
14. *Sphagnum quinquefarium*	*.12412*	−.07078	−*.33668*	.07327	−.06556
15. *Ptilidium ciliare*	−.00718	−.01639	.00460	−.00086	−.00604
16. *Picea abies* (seedling)	−.08383	.06267	−.10661	.11761	.05315
17. *Catharinea undulata*	.00201	−.00089	.01515	.01717	.00664
18. *Eurhynchium striatum*	.03392	*.23404*	*.33803*	−.03699	−*.58078*
19. *Mnium affine*	.02879	.00318	.13410	.17271	.13835
20. *Hedera helix*	.00087	.00034	.00446	.00519	.00208
21. *Viola silvatica*	.00007	.00035	.00088	.00031	−.00253
22. *Rhytidiadelphus loreus*	−.03664	.01352	−.00817	−.00246	.01330
23. *Lophocolea bidentata*	.00170	−.00654	−.03063	−.00306	.00739
24. *Dicranum scoparium*	.00937	−.00273	−.05384	.01676	−.00941
25. *Pleurozium schreberi*	−.06675	.12852	−.19156	*.20894*	.01655
26. *Bazzania trilobata*	*.23596*	−.10909	−*.56851*	.15899	−.14877
27. *Plagiothecium undulatum*	.00052	−.00125	.00378	−.00267	.00194
28. *Chiloscyphus polyanthemus*	.00147	−.00083	−.00278	−.00370	.00105
29. *Athyrium filix-femina*	−.00874	−.00791	.00104	−.00265	.00178
30. *Dicranella heteromalla*	.00046	.00021	−.00122	−.00107	.00104
31. *Agrostis tenuis*	−.00186	.00018	.00243	.00557	.00658
32. *Galium rotundifolium*	.00128	−.00081	.00066	−.00426	.00296
33. *Lophocolea heterophylla*	.00215	.00001	−.00358	−.00179	−.06340
34. *Mnium undulatum*	−.00234	−.00266	.00031	−.00098	.00064
35. *Abies alba*	*.58045*	−*.36666*	−.02491	−*.31329*	*.38070*
36. *Picea abies*	−*.48324*	*.34412*	−.17508	−*.27516*	*.42201*
37. *Fagus silvatica*	−.0237	−.15145	.08981	.06435	−.01536
38. *Quercus robur*	.01288	.01035	.06829	.06512	−.02768

component 3 and 4, *Polytrichum formosum* by component 1 and 2, *Eurhynchium striatum* by component 3 and 5, *Picea abies* by component 1, 2, and 5. The variation of *Bazzania trilobata* and *Sphagnum quinquefarium* can be described almost completely by component 3.

If the ecological requirements of the species are known, this can be an aid in explaining the possible ecological meaning of the axes to which these species are important contributors.

The projections of the points representing sample plots, on the planes spanning the first and second, and the first and the third principal axes, are shown in Fig. 14.
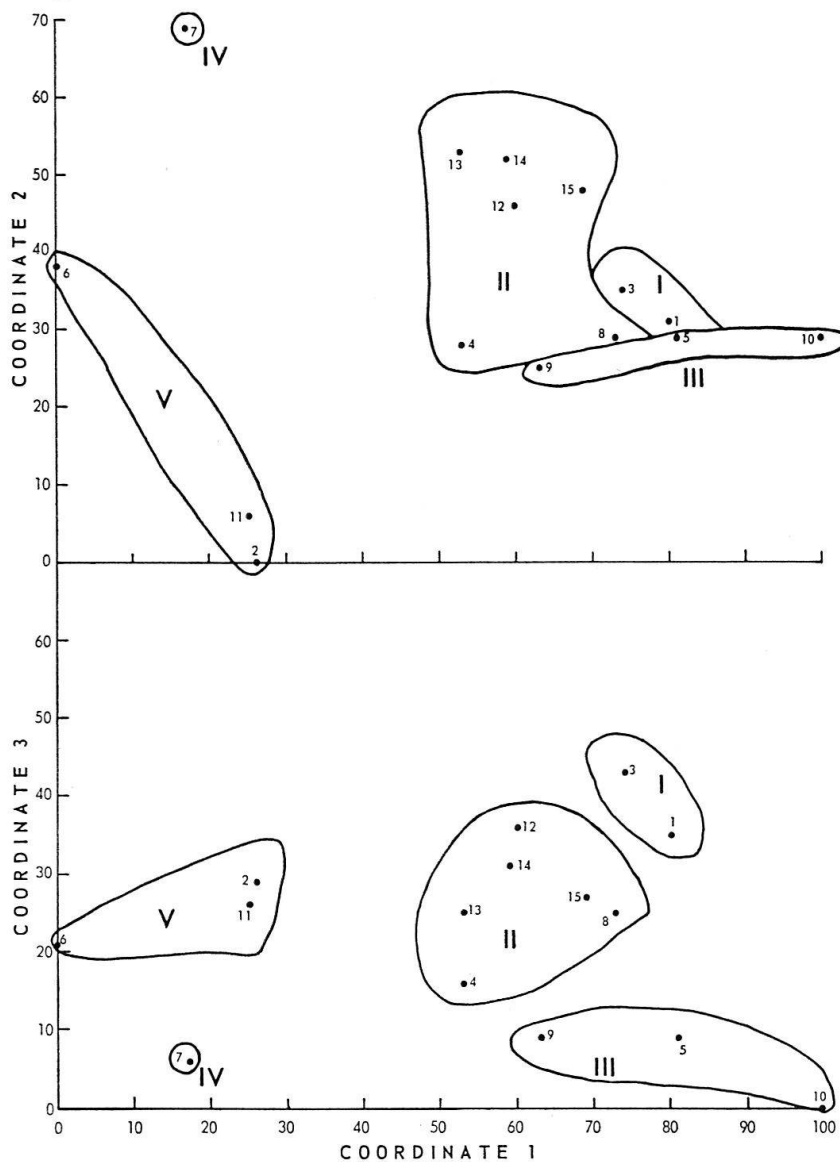

Fig. 14. Projection of sample plots on the planes spanning the first and second, and the first and third principal axes (covariance matrix, Swiss data) with clustering of plots indicated.

The relationships between the cover percentages of the more important species with the principal axes are shown in Fig. 15.

6.2.4 Habitat factors in relation to the principal axes

The habitat factors measured, light conditions and soil pH, were related to the principal axes. The "integrated light" levels and the soil pH on the sample
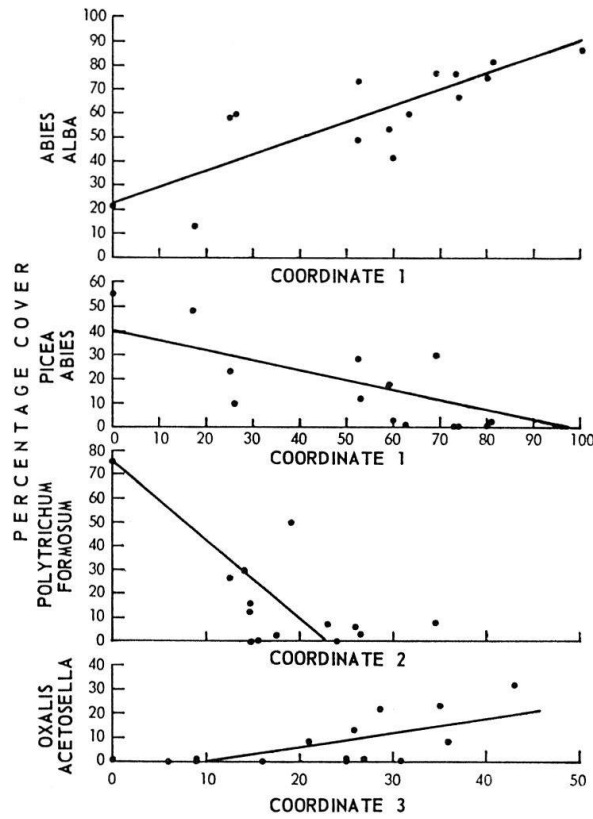

Fig. 15. Quantitative distribution of *Abies alba* and *Picea abies* along the first principal axis, *Polytrichum formosum* along the second principal axis and *Oxalis acetosella* along the third principal axis (cov. matrix, Swiss data).
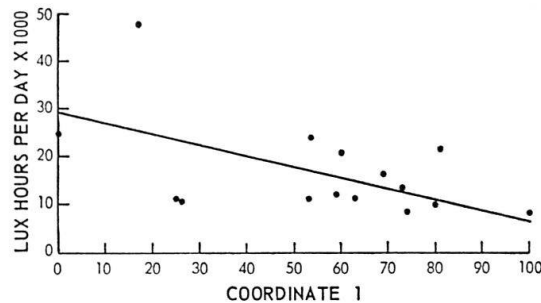

Fig. 16. Relationship between light conditions and the first principal axis (cov. matrix, Swiss data).

plots were plotted against the corresponding values (coordinates) of each plot, for each of the three principal axes. If any indication of a relationship existed, straight lines or regression curves were fitted.

Figs. 16 and 17 show the relationships of the first axis to light conditions and the third axis to soil pH. Both were statistically significant. No relationship was found with the second axis.
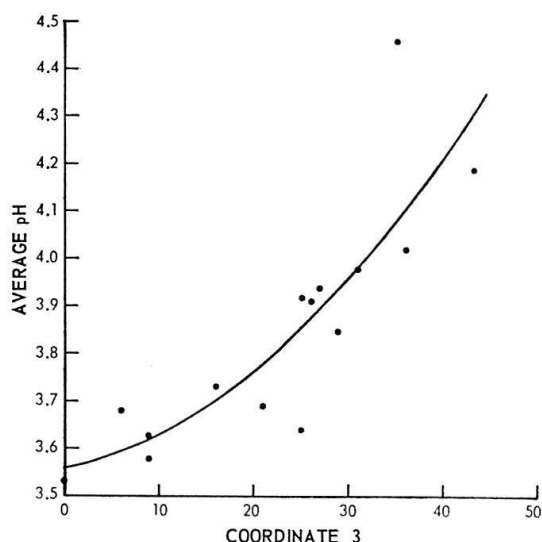

Fig. 17. Relationship between soil pH and the third principal axis (cov. matrix, Swiss data).

6.2.5 Analysis of the D^2 matrix

All D^2's were statistically significant ($P \leq .05$).

The D^2 matrix was investigated according to the method developed by Torgerson. Three axes were constructed and the points representing sample plots were projected on the planes spanning these axes (Fig. 18).

The distances in two-dimensional space were compared with the D^2's, by calculating the correlation coefficient between these distances and the corresponding D^2's. The correlation coefficient is .939, which is significant at the .001 level. Thus 88.7% of the variation is accounted for by the two dimensional ordination.

6.2.6 Habitat factors in relation to the main axes (D^2 matrix)

The relationship between each axis and the forementioned habitat factors was tested. As under paragraph 6.2.4, the first axis was significantly related only to light conditions (method 1) and the third axis to soil pH. Although the relationships were largely identical to those mentioned under paragraph 6.2.4, they were statistically less significant (Figs. 19 and 20).
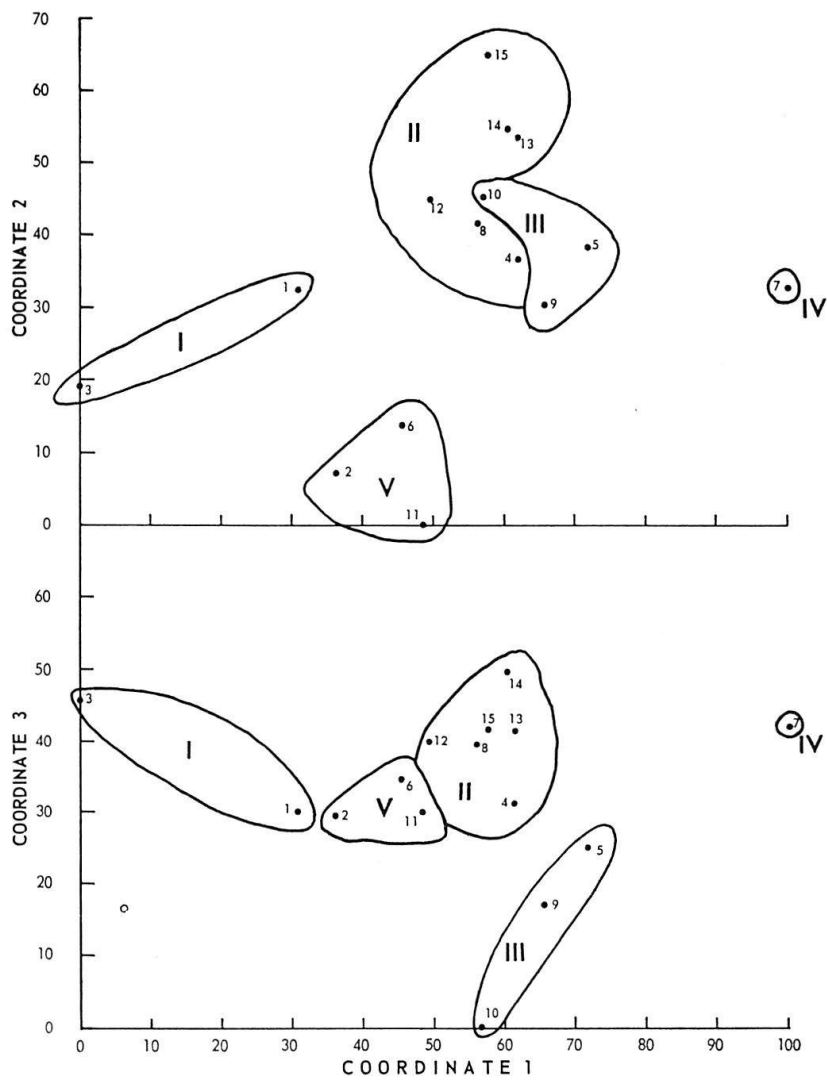
Fig. 18.   Projection of sample plots on the planes spanning the first and second, and the first and third main axes (D² ordination, Swiss data) with clustering of plots indicated.
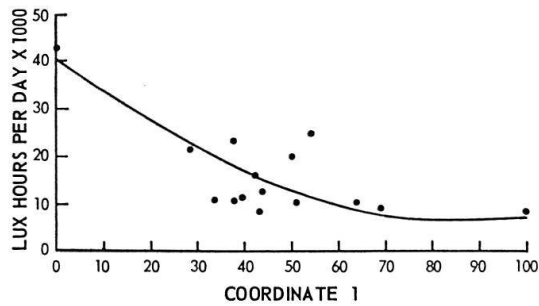

Fig. 19.   Relationship between light conditions and the first main axis (D² ordination, Swiss data).
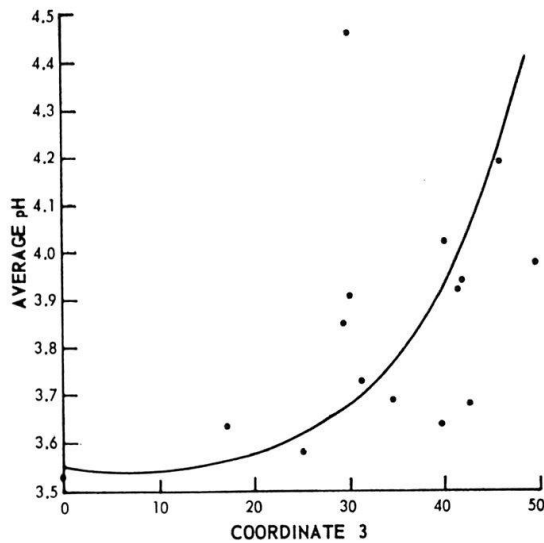
Fig. 20. Relationship between soil pH and the third main axis (D² ordination, Swiss data).

6.2.7 Principal component analysis (Q-method) of the transformed D² matrices.

Two transformations were used: $R = (1 + D^2)^{-1}$, and $R = e^{-D^2}$. The exponential subroutine used in Fortran on the G-20 computer, the $R = e^{-D^2}$ transformation works only with exponents between —63 and +63. Any exponent of which the absolute value was larger than 63 was automatically given the value 0. Since most of the off diagonal elements in the D² matrix were larger than 63 they were replaced by zeros in the transformed matrix. The resulting eigenvalues and eigenvectors were almost all zeros and ones. The results of this transformation were not analysed.

The results of the principal component analysis of the $R = (1 + D^2)^{-1}$ matrix are listed in table 2. Only the first three eigenvalues and the coefficients of their eigenvectors are listed.

The eigenvalues of the first three axes were as follows:

Trace of the matrix = sum of all eigenvalues = 15.0
Axes Eigenvalues

   I 1.1686522 accounting for 7.79% of the total variation.
  II 1.0373909 accounting for 6.92% of the total variation.
 III 1.0140313 accounting for 6.76% of the total variation.

The first two axes thus account for 14.71%, and the first three axes for 21.47% of the total variation.

Table 2. Eigenvalues and eigenvectors of the Swiss $(1 + D^2)^{-1}$ matrix.

		Axes				Axes	
	I	II	III	I		II	III
		Eigenvalues				Eigenvalues	
Plot	1.1686522	1.0373909	1.0140313		1.1686522	1.0373909	1.0140313
number		Eigenvectors		number		Eigenvectors	
1	.14222321	.17624994	.21756172	9	.25679214	.30200167	−.45595084
2	.12656551	.38099206	.35592580	10	.16825722	.21976787	−.42181803
3	.06633672	.15495798	.199353751	11	.13708974	.40578184	.31920601
4	.30028464	.19683786	−.27587316	12	.30902949	−.06469361	.12709984
5	.15062401	.19914597	.31330388	13	.45123823	−.28100184	.08031121
6	.14939449	.37723863	.28399513	14	.37905062	−.25283243	.07444108
7	.08432882	.12967207	−.08409874	15	.35159907	−.27186514	.09786224
8	.37135248	−.19260563	.03315040				

No projections of the plots on the planes spanning the first three axes are presented because they do not supply information not already contained in other figures and because these axes only account for a total of 21.47% of the total variation.

6.2.8 Habitat features in relation to the principal axes (Q-method)

The relationship between each axis and the habitat factors was tested. As before, the first axis was only significantly related to light conditions (method 1) and the third axis to soil pH. The relationships are expressed in Figs. 21 and 22.

6.2.9 Clustering of sample plots

The projection of the points, representing sampling plots, on the planes spanning the principal axes is shown in Fig. 14. There is a tendency to cluster, which coincides with that shown by the projection of the plots on the planes spanning the main axes of the hyper-space described by the D^2 matrix (Fig. 18). The clusters contain the following plots: Cluster I, plot 1 and 3; Cluster II, plot 4, 8, 12, 13, 14, and 15; cluster III, plot 5, 9, and 10; cluster IV, plot 7, and cluster V, plot 2, 6, and 11.

The D^2 matrix was analysed by the method developed by Tocher (Appendix III). This analysis showed the existence of five groups which were identical to the clusters mentioned before.

6.2.10 Habitat factors in relation to clustering of sample plots

The mean values of the habitat factors for each cluster were compared by "t" test, following an approximate method due to Cochran and Cox (GREIG-
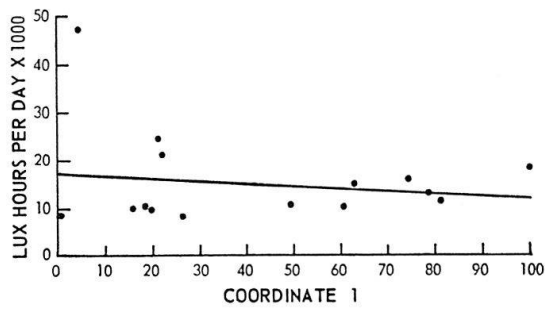
Fig. 21. Relationship between light conditions and the first principal axis $((1 + D^2)^{-1}$ matrix, Swiss data).
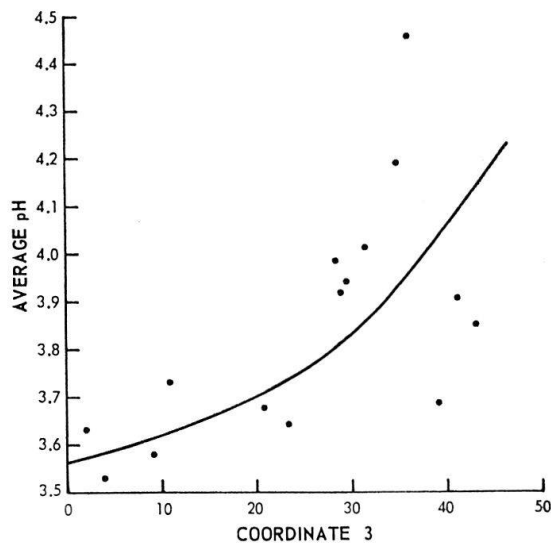

Fig. 22. Relationship between soil pH and the third principal axis $((1 + D^2)^{-1}$ matrix Swiss data).

SMITH 1964). The frequency distributions are close to normal, and no transformation was deemed necessary.

Most of the clusters have significantly different average light conditions. Not significant are the differences between the means of the levels of light received, of cluster I and III and of II and V. The average levels of light received by these sites with their standard deviations are 9.00 ± 1.56; 15.20 ± 12.43; 13.92 ± 10.45; 47.89 ± 24.51; and 16.92 ± 12.97 kilo-Lux hours per day respectively, at the time these measurements were made. The clusters are, with the exception of two, significantly different for soil pH's. The mean pH's with their standard deviations are $4.31 \pm .26$; $3.89 \pm .28$; $3.58 \pm .20$; 3.68 ± 1.17; and $3.81 \pm .31$ respectively. Clusters II and V with pH 3.89 and pH 3.81 respectively, which are not significantly different, occupy completely overlapping ranges along the third principal axis (covari-

ance matrix). Also cluster IV is not significantly different from clusters II, III, and V.

If the differences among the means are considered in relation to the sum of the standard deviations, only the differences among cluster I, II, and III and between cluster I and V carry weight.

6.3 Canadian sample plots

6.3.1 Classification of sample plots (Zürich-Montpellier method)

As is obvious from the plant tables (Appendix II), the vegetation of the white spruce forests in Saskatchewan is very homogeneous, with many species occurring in most of the plots. Nevertheless, it was possible to recognize, according to the differential species-group method, two groups of species which are predominantly present in a limited group of plots. These groups of species were used to group the plots into three units.

The first group (A) of species comprises: *Lonicera involucrata, Lonicera dioica, Ribes hirtellum, Ribes triste, Shepherdia canadensis, Amelanchier alnifolia, Lathyrus ochroleucus, Habenaria obtusata, Geocaulon lividum, Actaea rubra, Galium boreale* and the moss *Eurhynchium pulchellum*. These species were, with few exceptions, not present in the following plots: 1, 3, 5, 6, 7, 8, 13, 16, 19, and 38 (Vegetation unit III).

The second group (B) of species contains *Galium triflorum, Elymus innovatus, Equisetum scirpoides, Equisetum pratense, Hieracium canadense, Carex capillaris* and the lichen *Peltigera* spec. These species occurred predominantly in the following sample plots 9, 10, 11, 14, 22, 23, 27, 29, 31, 32, 35, 36, 37, and 43 (Vegetation unit I).

The species of group A did, and those of group B did not occur, in the following sample plots: 2, 4, 12, 15, 17, 18, 20, 21, 24, 25, 26, 28, 30, 33, 34, 39, 40, 41, and 42 (Vegetation unit II).

6.3.2 Habitat features in relation to classification of sample plots

The average level of each habitat feature for each vegetation unit, established in the foregoing paragraph, was compared statistically with those of the other two units with the following results. No significant differences were found among the average values of permanent wilting point (mean value with standard deviations in vegetation unit I, II, and III, respectively, 3.80 ± 1.96, 3.09 ± 1.16 and $2.86 \pm .99$), nitrogen content of the white spruce foliage ($1.26 \pm .04$, $1.25 \pm .06$, $1.24 \pm .09$), basal area of white spruce (139.9 ± 40.9, 137.9 ± 50.3, 139.3 ± 33.9), "measured mean" pH of the mineral soil (4.95 ± 1.15, 4.94 ± 1.14, 4.71 ± 1.26), "measured mean" pH of

humus layer (5.63 ± .53, 5.45 ± .53, 5.09 ± .7), "measured mean" pH of the fermentation layer (5.92 ± .48, 5.99 ± .28, 5.56 ± .47).

Significant differences (at P = .05) were found among the average levels of the field capacity (unit II and III), "available moisture" (unit I and III) and height growth (I.H.G.I.) (unit I and III). The average levels for the three units are as follows: field capacity: 15.20 ± 2.05, 15.36 ± 1.30, and 16.85 ± 2.16; "available moisture": 11.52 ± 2.04, 12.06 ± .95 and 13.93 ± 2.03; I.H.G.I.: 1.075 ± .19, 1.10 ± .15 and 1.18 ± .24.

The significant differences between the average levels of "available moisture" and height growth in units I and III suggest that height growth is correlated with the available moisture. To test this relationship further, all levels of available moisture were plotted against the corresponding levels of height-growth and a correlation coefficient was calculated. No statistically significant relationship was found to exist (r = .20, P > .10). A relationship did exist, if only the sample plots contained in unit I and III were used (r = .40, P = .05).

Table 3. Eigenvalues and eigenvectors of the Canadian covariance matrix.

	Axes				
	I	II	III	IV	V
Eigenvalues	34419	7106.4	3483.3	2945.5	1405.6
Species			Eigenvectors		
1. *Rosa acicularis*	.02997	−.00142	−.04535	−.02109	−.04783
2. *Linnaea bor.* var. *amer.*	.08841	.09679	−.57951	−.23789	−.42702
3. *Petasites palmatus*	.05866	−.01554	−.32896	.03517	.22979
4. *Cornus canadensis*	.18676	−.07685	−.53373	.14256	.31060
5. *Fragaria vesca*	.00366	.00123	−.00638	−.01131	.01474
6. *Fragaria virginiana*	.06284	−.00548	−.10823	.03739	.12304
7. *Mitella nuda*	.01005	.01577	−.10223	−.02328	.13508
8. *Mertensia paniculata*	.10699	−.04036	−.22644	.02635	.37971
9. *Maianthemum canadense*	.02280	−.00705	−.11046	−.01176	.01194
10. *Pyrola secunda*	.00624	−.00321	−.00928	−.00692	−.00755
11. *Aralia nudicaulis*	.03371	−.01406	−.07949	.04377	−.02303
12. *Vaccinium v.id.v.m.*	.00004	.00017	−.00065	.00014	.00059
13. *Pyrola virens*	−.00300	−.00301	−.01792	−.00354	.00075
14. *Trientalis borealis*	.00634	−.00097	−.04825	.00843	−.02151
15. *Rubus pubescens*	.05164	−.02624	−.18379	.03222	.16242
16. *Hylocomium splendens*	−.78547	−.39106	−.21676	.40044	−.10261
17. *Pleurozium schreberi*	−.28288	.87947	−.07136	.32474	.15732
18. *Cornus stolonifera*	.00677	.00454	.00277	−.00122	.02461
19. *Symphoricarpus alba*	.00277	.00404	.00297	−.01089	.01708
20. *Picea glauca*	−.33991	−.06533	.13128	.54098	.60846
21. *Populus tremuloides*	.34709	−.22530	.21387	.59620	.23259
22. *Populus balsamifera*	.00076	−.01140	.06081	−.03706	−.0159

6.3.3 Principal component analysis of the covariance matrix

The principal component analysis resulted in principal axes with the following eigenvalues.

Trace of the matrix = sum of all eigenvalues = 51859.0

Axes Eigenvalues

I 34419.0 accounting for 66.3% of the total variation.

II 7106.4 accounting for 13.7% of the total variation.

III 3483.3 accounting for 6.7% of the total variation.

IV 2945.5 accounting for 2.7% of the total variation.

The first two axes account for 80.0%, the first three axes for 86.7%, the first five axes for 95,1% on the total variation.

The eigenvalues and coefficients of the eigenvectors are listed in table 3. The coefficients which contribute the most are in italics.
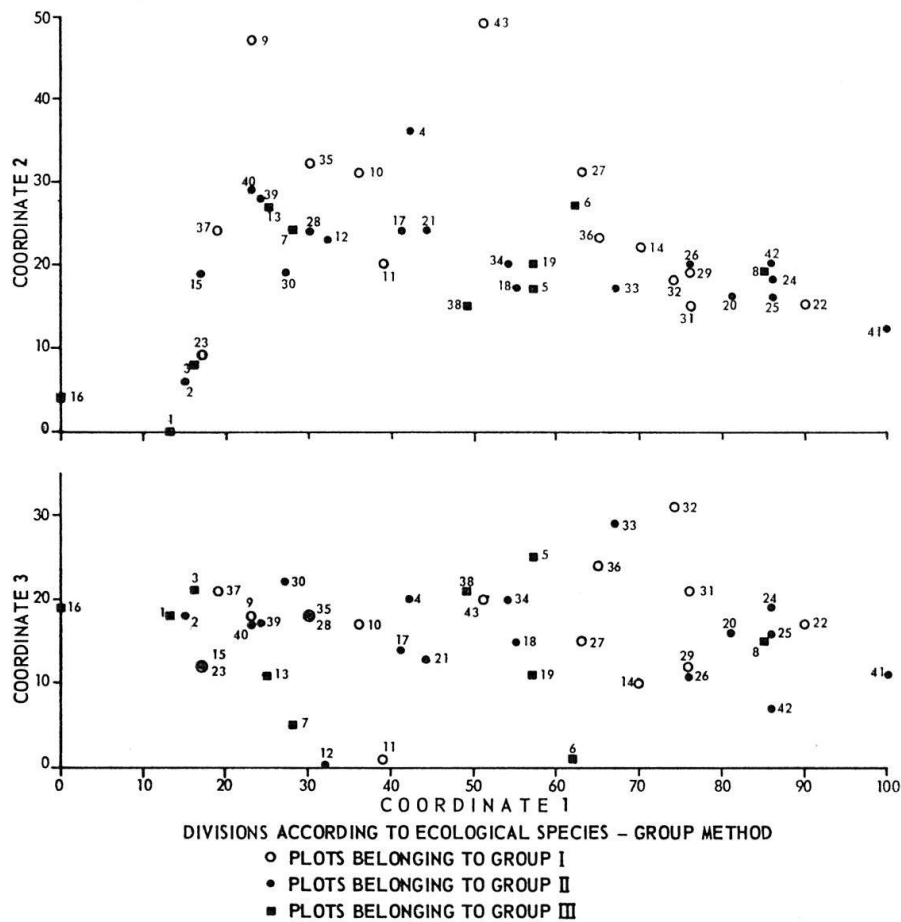
Fig. 23.   Projection of sample plots on the planes spanning the first and second, and the first and third principal axes (cov. matrix, Canadian data) with classification of sample plots according to the differential species-group method, indicated.

As in table 1, it is noticeable that the variance of several species can only be explained by more than one component. The fourth and fifth components, however, have such low eigenvalues that for all practical purposes they can be omitted. On this basis the variance of *Linnaea borealis* var. *americana*, *Petasites palmatus*, *Cornus canadensis*, *Mertensia paniculata* and perhaps *Rubus pubescens* can be explained by component 3 and *Picea glauca* by component 1.

The variance of *Hylocomium splendens* and *Pleurozium schreberi* can only be explained by components 1 and 2. To explain the variance of *Populus tremuloides* all of the first three components are needed.

The projections of the points representing sample plots, on the planes spanning the first and second, and the first and third principal axes are shown in Fig. 23.

The relationships between the cover percentages for the more important species and the principal axes are shown in Figs. 24 to 27 inclusive.

6.3.4 Habitat features in relation to the principal axes

The habitat features measured, mentioned under Methods, were related to the principal axes. When the graphs indicated a possible significant relationship either a straight line or a curve was fitted to the data.
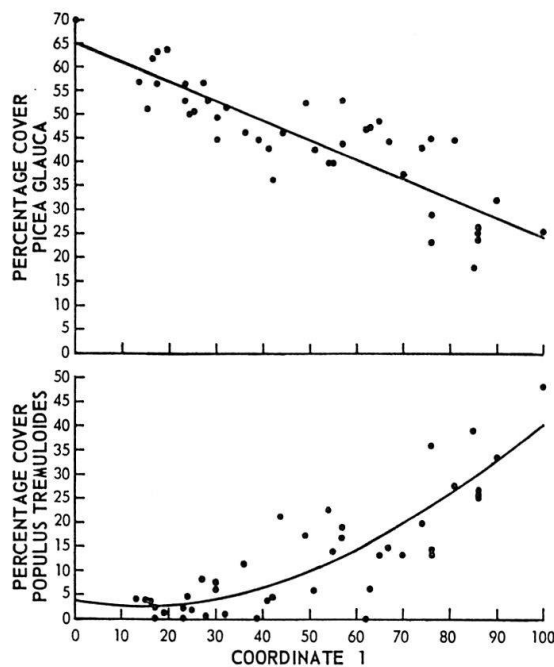

Fig. 24. Quantitative distribution of *Picea glauca* and *Populus tremuloides* along the first principal axis (cov. matrix, Canadian data).
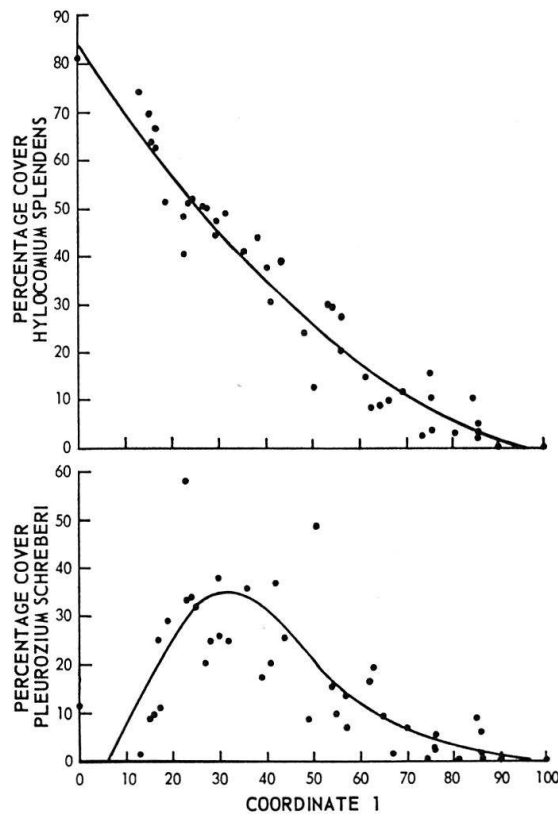
Fig. 25. Quantitative distribution of *Hylocomium splendens* and *Pleurozium schreberi* along the first principal axis (cov. matrix, Canadian data).
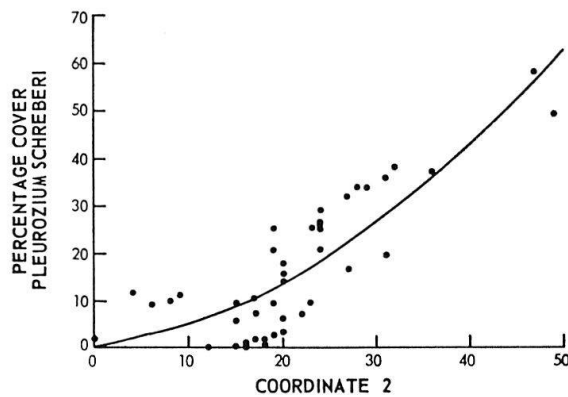

Fig. 26. Quantitative distribution of *Pleurozium schreberi* along the second principa axis (cov. matrix, Canadian data).

Basal area of white spruce, maximum pH of the humus layer, maximum pH of the top mineral soil, and the "measured mean" pH of the fermentation layer were all significantly linearly related to the first principal axis, with correlation coefficients, $r_{BA} = -.745$, $P = .001$; $r_{pH,H.} = -.56$, $P = .001$;
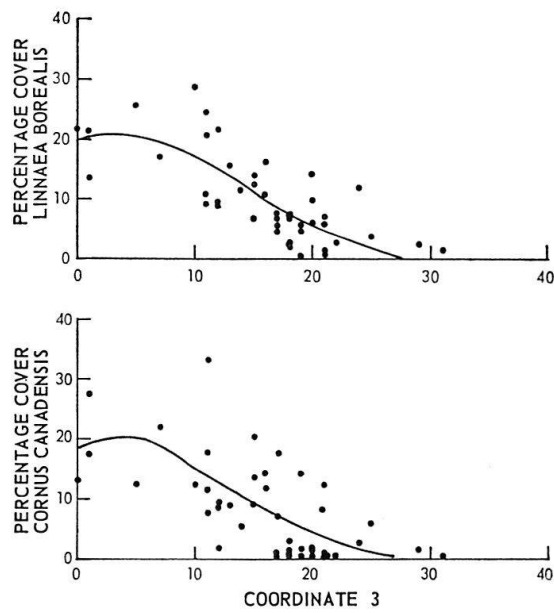
Fig. 27. Quantitative distribution of *Linnaea borealis* and *Cornus canadensis* along the third principal axis (cov. matrix, Canadian data).
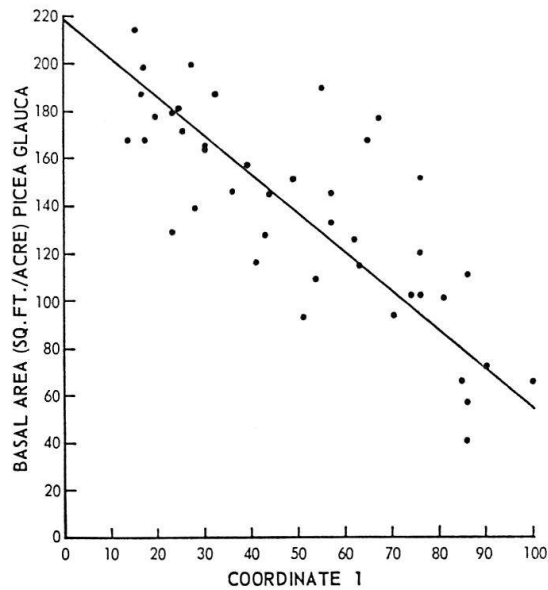

Fig. 28. Relationship between the basal area (sq. ft./acre) of *Picea glauca* and the first principal axis (cov. matrix, Canadian data).

$r_{pH,s.} = -.30$, $P = .05$; and $r_{pH,F.} = .62$, $P = .001$ (Figs. 28, 29, 30, and 31). No other features showed a significant relationship with the first axis.

Only "available moisture" (% dry weight) was linearly related to the second principal axis, $r = -.50$, $P = .001$ (Fig. 32). No other features showed a significant relationship to the second axis.
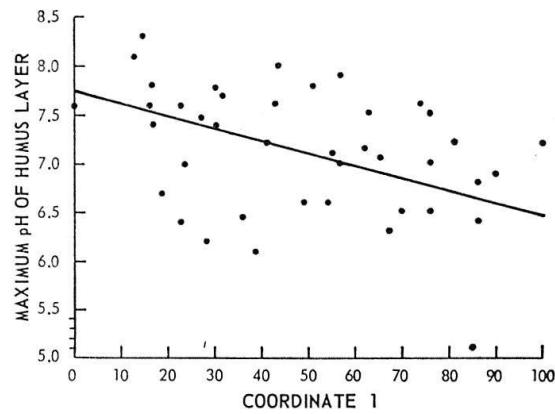
Fig. 29. Relationship between the maximum pH of the humus layer and the first principal axis (cov. matrix, Canadian data).
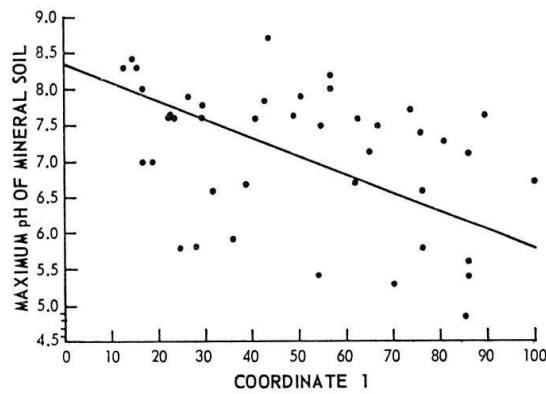

Fig. 30. Relationship between the maximum pH of the top of the mineral soil and the first principal axis (cov. matrix, Canadian data).
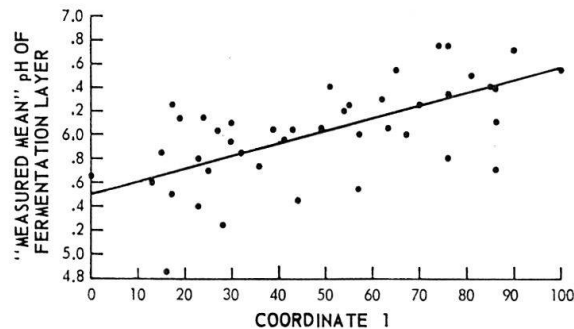

Fig. 31. Relationship between the "measured mean" pH of the fermentation layer and the first principal axis (cov. matrix, Canadian data).

The "measured mean" pH of the humus layer was significantly related to the third principal axis, $r_{pH, H.} = .32$, $P = .05$ (Fig. 33).

Contrary to expectations, no relationships were found with either the height-growth of white spruce, the nitrogen content of the white spruce foliage, field capacity, or permanent wilting point.
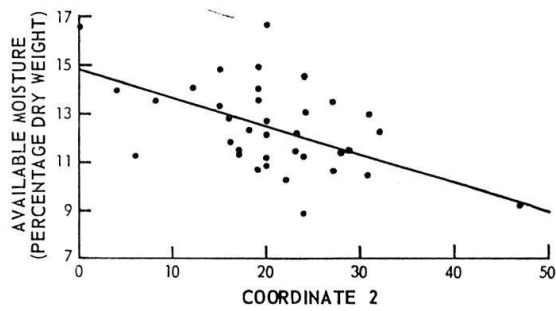
Fig.32. Relationship between the "available moisture" and the second principal axis (cov. matrix, Canadian data).
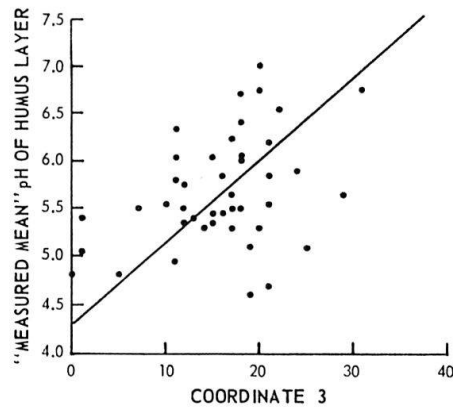

Fig.33. Relationship between the "measured mean" pH of the humus layer and the third principal axis (cov. matrix, Canadian data).

6.3.5 Analysis of the D^2 matrix

The D^2 matrix was investigated according to a method developed by Torgerson.

The first two axes were constructed and the points representing sample plots were projected on the plane spanning these axes (Fig.34).

The distances between the points in the one and two dimensional projections, respectively, were correlated with the corresponding D^2's. The correlation coefficients were .777 and .854 respectively. Both correlation coefficients were significant of the 0.1% level. This means that the first axis accounts for 60.37% of the variation present in the D^2 matrix. The two axes account for 72.93% of the variation.

6.3.6 Habitat features in relation to the main axes

The relationships between the above mentioned axes and habitat features were investigated. The graphs closely resembled those found with the principal axes (R method) but the relationships were slightly less significant, e.g. the correlation coefficient expressing the relationship between the first main
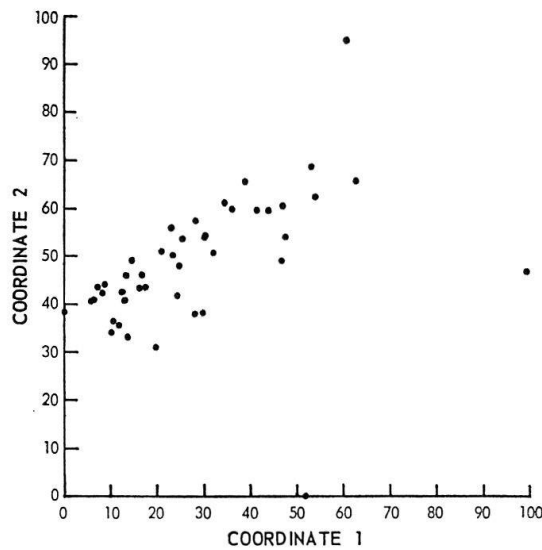
Fig. 34. Projection of the sample plots on the plane spanning the first and second main axes (D^2 ordination, Canadian data).
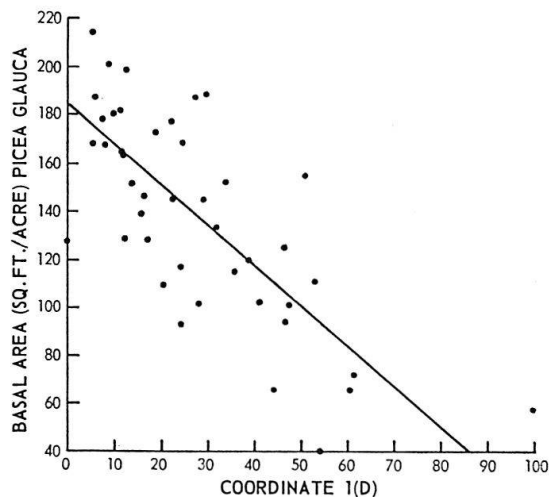

Fig. 35. Relationship between the basal area (sq. ft./acre) of *Picea glauca* and the first main axis (D^2 ordination, Canadian data).

axis and the basal area of the white spruce was $-.725$ (Fig. 35). No figures (except Fig. 35) are shown here because the graphs do not convey any information not already contained in Figs. 24 to 27 inclusive.

6.3.7 Principal component analysis (Q-method) of transformed D^2 matrices

The transformation, $R = e^{-D^2}$, was not successful for the reasons mentioned before (paragraph 6.2.7).

The first three eigenvalues and the coefficients of their eigenvectors resulting from the principal component analysis of the $(1 + D^2)^{-1}$ matrix are listed in Table 4.

Table 4.   Eigenvalues and eigenvectors of the Canadian $(1 + D^2)^{-1}$ matrix.

		Axes				Axes	
	I	II	III		I	II	III
		Eigenvalues				Eigenvalues	
Plot number	4.0806686	1.8414362	1.6545757	Plot number	4.0806686	1.8414362	1.6545757
		Eigenvectors				Eigenvectors	
1	.20518162	.32619265	−.32774792	23	.15197713	.02036635	−.06348675
2	.24044327	.32953310	−.23929013	24	.04943476	−.124469254	−.12125866
3	.25562373	.34163588	−.22040681	25	.05120825	−.13622218	−.12974217
4	.16712484	−.12401396	.14859947	26	.06658242	−.16450270	−.14332642
5	.13033962	−.19461947	−.18080734	27	.06418442	−.11944390	−.07672237
6	.03592506	−.06887253	−.05870816	28	.28425387	.02207873	.21035904
7	.11047054	−.09594629	−.03622257	29	.06327470	−.14348925	−.12240309
8	.05520553	−.13105740	−.12363875	30	.29817677	1.17514492	.07243274
9	.14213920	−.07366455	.19829468	31	.08458285	−.17758661	−.16518164
10	.22174998	−.09770317	.20514791	32	.08849949	−.18908332	−.17954269
11	.02789219	−.04236062	−.03669437	33	.05794918	−.09023190	−.10923668
12	.05505172	−.07654838	−.04998491	34	.15478582	−.18599630	−.10503147
13	.14705452	−.06792552	.03131438	35	.25702541	−.06008116	.33602007
14	.05373110	−.11997895	−.10965319	36	.11933932	−.23806116	−.19634325
15	.19527573	.04616300	.03421793	37	.27149510	.12739532	.17038237
16	.18256004	.28617043	−.23673914	38	.13846497	−.13885203	−.13263136
17	.16980892	−.13020093	.00813848	39	.19590994	−.02729770	.16600462
18	.07005728	−.11537413	−.10632461	40	.25495578	−.02206047	.28823524
19	.05662565	−.18391777	−.11756376	41	.02713084	−.06485623	−.06370964
20	.04151320	−.09466050	−.08648553	42	.02023899	−.04192575	−.03992062
21	.11655024	−.13487681	−.05092089	43	.10970964	−.13128951	.07590625
22	.03776468	−.09555740	−.09051711				

Trace of the matrix = sum of all eigenvalues = 43. Eigenvalue I is 4.0806686 and thus accounts for 9.49% of the total variation,

Eigenvalue II is 1.8414362 and accounts for 4.28% of the total variation,

Eigenvalue III is 1.6545757 and accounts for 3.85% of the total variation.

The first two axes thus account for 13.77%, and the first three axes for 17.62% of the total variation.

For comparison only, the relationships of *Picea glauca* and *Hylocomium splendens* with the first principal axis are shown (Figs. 36 and 37).

Projections of the plots on the planes spanning the principal axes are not shown for the same reasons mentioned under paragraph 6.2.7.

6.3.8 Habitat features in relation to principal axes (Q-method)

The habitat features were related to the principal axes mentioned above. They were found to be similar to the relationships described before. For comparison, the relationships of the basal area of *Picea glauca* with the first axis is shown in Fig. 38. The correlation coefficient was calculated to be .592 which is significant at the 0.1% level.
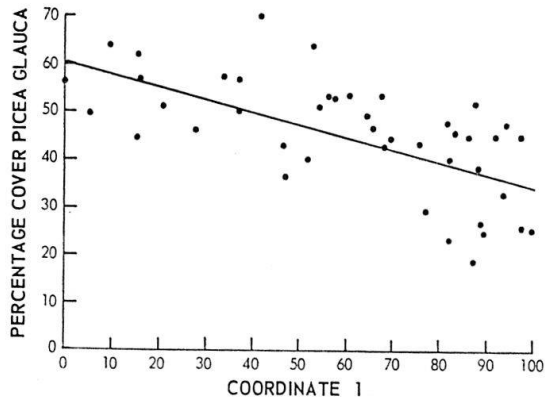
Fig. 36. Quantitative distribution of *Picea glauca* along the first principal axis ((1 + D²)⁻¹ matrix, Canadian data).
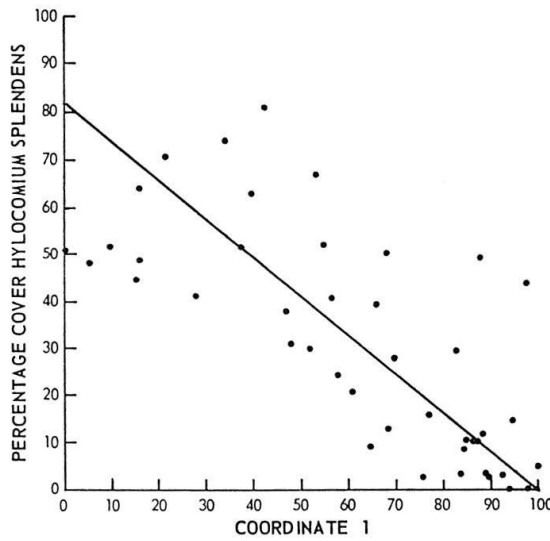

Fig. 37. Quantitative distribution of *Hylocomium splendens* along the first principal axis ((1 + D²)⁻¹ matrix, Canadian data).
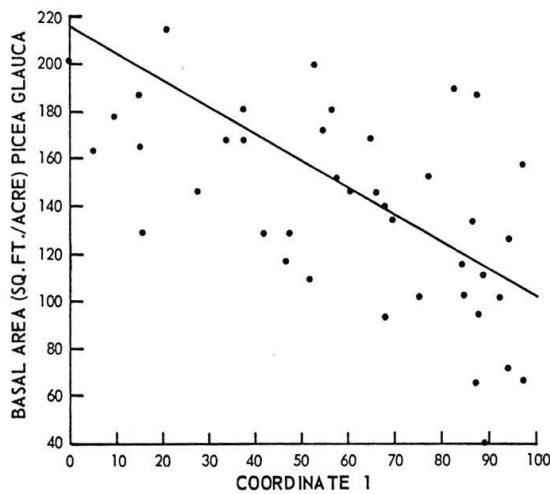

Fig. 38. Relationship between the basal area (sq. ft./acre) of *Picea glauca* and the first principal axis ((1 + D²)⁻¹ matrix, Canadian data).

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.