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A CLASSIFICATION-ORDINATION ANALYSIS OF A BELGIAN MIXED FOREST IN THE TRANSITION ZONE OF TWO PHYTOGEOGRAPHICAL DISTRICTS. II. SPRING DATA *

P. Van Hecke, I. Impens & T. Van Tilborgh **

Departement Biologie, Universitaire Instelling Antwerpen,
B - 2610 Wilrijk, Belgium.

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Introduction

As already mentioned in a previous paper in which the summer data were discussed (Van Hecke et al. 1976) the need was felt to analyse also the spring data, due to the fact that this forest distinctly shows two seasonal aspects.

Consequently the results of the two studies will be compared.

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* Plant nomenclature follows De Langhe et al. (1973)

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Study area and sampling methods.

For a description of the study area: see Van Hecke et al. (1976).

Spring data are restricted to the moss layer, the lower herb layer (LHL: on the average less than 20 cm), the upper herb layer (UHL: on the average more than 20 cm) and the litter: information on the two tree layers and the shrub layer was discarded.

About mid-April 1976 115 quadrats of 7 m x 7 m were systematically laid out precisely on the same places as the summer quadrats in 1974. (For their coordinates, see Van Hecke et al. 1976).

For each relevé and each layer were recorded: 1) the real cover (Barkman et al. 1964) of all vascular species (58 taxa: Tab. 1) and of the bryophytes (handled as an anonymous group of species) on the altered Blaun-Blanquet scale (-1%, 1%, 3%, 5%, 15%,35%, 60% and 85 %); 2) the total cover and height of each layer and 3) the height of the litter.

Following the Flora-list of Van der Maarel (K.U. Nijmegen) each taxon was characterized with a code-number for computer analysis.

Both herb layers were totally lacking in quadrat nr. 98.

1. Classification techniques.

1.1. Unweighted pair-group centroid method (UPGC)

As compared to the previous paper, this analysis, now operational as the program CLUSWEC, remained unchanged.

1.2. Association analysis (NAA)

The normal or Q-mode analysis was applied (program NOAS) either to all taxa or to those with a constancy degree between 5 and 95%, i.e. 26 instead of 58 taxa. The splitting up of the groups of relevés was carried out either with the highest $\Sigma|V|$ or χ^2, combined with a probability level of 1% ($\chi_1^2 = 6.64$) or 5% ($\chi_1^2 = 3.84$).

1.3. Information analysis (IA)

An analysis in Q-mode (normal - IA or NIA) and in R-mode (inverse IA or IIA) was applied in the agglomerative way: those two relevés or groups of relevés are to be combined whose union produces the smallest gain in information content. While in this case precense/absence data are computed, the same set of data was analysed in the quantitative way as described by Dale (1971) using the formula

$$I = p \times n \times \log_e n - \sum_{j=1}^{p} \left[a_j \times \log_e a_j + (n-a_j)\log_e(n-a_j)\right] \qquad (1)$$

where p = the number of different taxa, n = the number of different relevés as compared with each other (qualitatively) or the number of subunits (100 or a multiple of it; quantitatively), a_j = the number of quadrats with the jth taxon (qualitatively) or the number of subunits with the jth taxon (the cover percentage or their sum in the jth taxon; quantitatively).

1.4. Minimum variance clustering (MVC)

In this sum of squares method of Orloci (1967 and 1978) fusions are only carried out when the within group s.o.s. has been minimized and alternatively the between group s.o.s. maximized.

Fusion of vegetation relevés starts with the computation of the squared Euclidean distance between each pair of quadrats with normalized data:

$$d^2(j,k) = \frac{1}{p} \sum_{i=1}^{p} \left[\frac{x_{ij}}{\nu_j} - \frac{x_{ik}}{\nu_k}\right]^2 \qquad (2)$$

where x_{ij} and x_{ik} are the values of the ith-species in the relevés j and k respectively, p the number of species and

$$\nu_j = \left[\sum_{i=1}^{p} x_{ij}^2\right]^{1/2} \qquad \text{and} \quad \nu_k = \left[\sum_{i=1}^{p} x_{ik}^2\right]^{1/2} \qquad (3)$$

From the generated D^2-matrix, several Q-matrices are computed, each time preceded by the computation of the s.o.s. or clustering criterion defined as

$$Q_{AB} = \frac{N_A N_B}{N_A + N_B} d^2(A,B) \qquad (4)$$

where N_A and N_B are the number of quadrats or characters in cluster A and B for the minimum Q-value. The fusion-levels in the dendrogram are dictated by the within group s.o.s.

For the clustering of structure-relevés, the raw data are normalized (formulas 3) and the distance computed with the Canberra metric:

$$d_{CANB(j,k)} = \frac{1}{p} \sum_{i=1}^{p} \frac{|x_{ij} - x_{ik}|}{x_{ij} + x_{ik}} \qquad (5)$$

where p is the number of structural features. The result is a D-matrix.

In grouping the taxa, the raw data were neither transformed nor standardized, but the same phi-coefficient was used as for the Hierarchical Grouping method in the previous paper resulting in a ϕ-matrix.

To determine the optimal number of clusters, this MINVAC-program contains also the formula of Beale (Kendall 1972). According to Hogeweg (1976) an alternate formula is

$$H = \frac{\sum_{i=1}^{c} I_i}{\sum_{i=1}^{c} R_i} \qquad (6)$$

where c is the fixed maximal number of clusters, I_i the between cluster ultrametric distance and R_i the within cluster ultrametric distance. As well B_{max} as H_{max} are giving the optimal number of clusters.

2. Ordination techniques.

2.1. Polar ordination (Bray & Curtis) modified by Beals (1965) (POB)

For this and the following ordination techniques the data were always quantitatively analysed.

After double standardization of the raw data, the index of similarity is computed as

$$IS = \Sigma w \qquad (7)$$

where w is the smaller value of the species common in any relevés-pair while the index of dissimilarity ID = 100 - IS. The first reference quadrat (A) on the X-axis is the one with the lowest sum of similarities, the second (B) is the one with highest dissimilarity with quadrat (A). The first reference relevé (C) on the Y-axis shows the highest value of $e^2 = D_a^2 - x^2$ (8) where D_a the dissimilarity is of a given quadrat from the first reference quadrat and x the value of that quadrat along the X-axis); the second reference relevé (D) is the one with the highest dissimilarity with relevé (C) and which has a cotangent greater than 5.67, thus showing a deviation from the perpendicular of no more than 10°. The reference relevés (E and F) for the Z-axis were chosen by inspecting all pairs of quadrats within 10% of each other in the two dimensions and with a cotangent greater than 5.67; the pair with highest dissimilarity is then selected (program PORCOT).

2.2. Simple ordination or the method of the perpendicular axes (SO)

Our program SOR adapted after Orloci (1966), transforms the raw data by $\log_2 (n + 1)$ and computes the distances between quadrats, taxa or structural characters by the Euclidean Distance:

$$D^2_{jh} = \sum_{i=1}^{N} \left[x_{ij} - x_{ih} \right]^2 \tag{9}$$

where x_{ij} and x_{ih} are the values of the ith variable in the individuals j and h, and N the total number of variables or individuals. Both reference points (R1 and R2) on the X-axis are those with the highest value in the D^2-matrix.

The first reference point (R3) on the Y-axis is found by the highest value of $h^2_j = D^2_{1j} - x'^2_{1j}$ (10; cfr.section 2.1.), while the analogous point (R4) on the Z-axis is derived from the highest value of $q_j =$

$$\left[D^2_{1j} - x'^2_{1j} - x'^2_{2j} \right]^{1/2} \tag{11}$$

where D^2_{1j} is the distance between R_1 and the jth character, x'^2_{1j} and x'^2_{2j} the distances on the X-axis between the j th character and the reference points R_1 and R_2.

The efficiency of the k th axis is given by the ratio:

$$\frac{\sum_{j=1}^{N-1} \sum_{h=j+1}^{N} d^2_{kjh}}{\sum_{j=1}^{N-1} \sum_{h=j+1}^{N} D^2_{jh}} \tag{12}$$

where $d_{kjh} = x'_{kj} - x'_{kh}$; self comparisons are excluded.

2.3. Optimized polar ordination (OPO)

The rpogram OPPOR includes this ordination technique, for the first time described by Swan, Dix & Wehrhahn (1969).

In contrast to Simple Ordination, which uses the distant character (= quadrat, taxon, structural character) as a criterion for axis selection this analysis chooses as first axis the one accounting for the highest proportion of the sum of squares for all intercharacter distances, while the second and subsequent axes are selected as the orthogonal components which account best for the residual sum of squares.

This sum of squares for the X-axis is computed as

$$S.S_x = \Sigma \alpha^2 - \frac{(\Sigma\alpha)^2}{P} \qquad (13)$$

with P being the number of characters, and

$$\alpha = \frac{d^2_{AB} + d^2_{AP} - d^2_{BP}}{2d_{AB}} \qquad (14)$$

d^2_{AB} the matrix distance between the two reference points A and B of the X-axis and d^2_{AP} and d^2_{BP} the matrix distances between a third character P and the two reference points A and B.

The efficiency or percent extraction value for the k th axis is given by

$$\frac{2\,P \times S.S_k}{\sum\limits_{ij} d^2_{ij}} \qquad (15)$$

Other parts of the procedure resemble the computation technique prescribed by the SO-method, including the data transformation by $\log_2 (n+1)$.

2.4. Position vectors ordination (PVO)

According to Orloci (1966, 1978) the sites (relevês, taxa, structural characters) are defined in terms of position vectors which represent directed lines to the sites (as points flattened into Euclidean planes) from the centroid [illegible] space, i.e. the center of gravity of all points. The first axis coincides with the position vector on which the sum of squared projections of all position vectors is maximum.

From a matrix X of data, transformed by $\log_2 (x+1)$, a matrix A is computed, using the formula

$$a_{ij} = \frac{x_{ij} - \bar{x}_i}{S_i} \tag{16}$$

where a_{ij} is the value of the ith variable in the j th individual in matrix A, x_{ij} the same value in matrix X, $\bar{x}_i$ the mean of the i th variable in all individuals and S_i "a factor of standardization chosen by the phytosociologist" (Orloci 1973:265). S_i here is taken as 1. A new matrix Q = A'A is generated.

Each position vector, identified by the property $S_h = \sum_j q^2_{jh}/q_{hh}$ (where $j,h = 1,2,\ldots,n$), is partitioned into two orthogonal components.

After detecting the maximum $S_h (=S_m)$ and computing the first set of co-ordinates by the property $Y_1 = q_{mh}/\sqrt{q_{mm}}$ (where $h = 1,2,\ldots,n$), the residual component is used to compute a residual matrix in order to obtain the subsequent axes. The procedure automatically stops when a residual matrix is a zero matrix. The program PVOR again gives a measure of efficiency of the kth axis by the ratio:

$$\frac{\sum\limits_{j=1}^{N} Y^2_{kj}}{\sum\limits_{j=1}^{N} q_{jj}} \tag{17}$$

where Y_{kj} is the jth co-ordinate on the kth axis, N the total number of variables or individuals and q_{jj} an element in the principal diagonal of Q.

All computations were carried out on the PDP 11/45 computer of the Universitaire Instelling Antwerpen.

3. Comparison of the results within each technique.

3.1. Classification techniques.

3.1.1. Unweighted pair-group centroid method (UPGC)

Because the number of taxa in this data-set was much lower, as compared to the summer data, all taxa were involved. Since determination was restricted to Phanerogams, taxa could only be found in two layers.

Clustering the relevés according to the taxa, the picture is very confused (Fig. 7): only the clear-cut, the wet W-corner and parts of certain forest-paths are well detected. These forest elements are particularly characterized by the presence of Carex pilulifera and Pteridium aquilinum (clear-cut), the presence of Heracleum sphondylium, Poa compressa, Stellaria holostea and Urtica dioica (forest-paths), the absence of them (W-corner).

The picture given by the clustering of structure-relevés is also partially confusing: many reversals hampering the interpretation are noted. Moreover, the height seems to play an unimportant role in the clustering. For practical purposes the identification of seven clusters is not possible at the same similarity-level. They are roughly characterized as follows: cluster 1 (24 relev.), with on the average a LHL of 2,5% cover and a UHL of 15% cover, is nearly restricted to the clear-cut; cluster 2 (the largest part of the forest, 61 relev.) is practically impossible to interpret, not even the smaller sub-clusters; cluster 3 (2relev.!) with no moss layer and a thin litter, maximally up to 5 cm; cluster 4 (6 relev.: the wet W-corner and some parts of forest-paths with a LHL covering 60% or 85% and an UHL with a cover up to 5%; cluster 5 (4 relev.) with a LHL covering 35 or 60% and with no UHL; cluster 6 (5relev.) with no moss layer and a litter thicker than 5 cm; cluster 7 (11 relev.) with a LHL maximally covering up to 5% and no UHL.

The similarities between the species are low to very low, again usually less than 30%. Typical groups of species can not be detected.

3.1.2. Normal association analysis (NAA)

For a first analysis, all taxa were involved, while the splitting up of groups was carried out with the max. Σ|V| combined with stopping rules at 5 and 1% respectively.

With the 5% stopping rule (Fig. 1), the delimitation in seven clusters seems appropriate: cluster 1 (4 relev.) is characterized by Aegopodium podagraria, cluster 2 (17 relev.; the wet W-corner and a considerable part along the brooklet) by Ranunculus ficaria, cluster 3 (22 relev.: especially two interior parts of the forest) by Lamium galeobdolon and Polygonatum multiflorum, cluster 4 (11 relev.) by L. galeobdolon and by the absence of P. multiflorum, cluster 5 (9relev.; the clear-cut) by Deschampsia cespitosa, cluster 6 (21 relev.; dominant especially in the southern area of the forest) by Anemone nemorosa and cluster 7 (29 relev.: especially the dry N-corner, the SE-border of the forest and the SE-one of the clear-cut) by the absence of all species just mentioned.

With the 1% stopping rule (Fig. 2), partitioning in seven clusters seems again to be appropriate: cluster 1 (9 relev.) is characterized by Heracleum sphondylium and resembles much the former clusters 1 and partially 2; cluster 2 (12 relev.), with R. ficaria resembles partially the former cluster 2; cluster 3 (20 relev.) with A.nemorosa, P. multiflorum and L. galeobdolon is very similar to the former cluster 3; cluster 4 (15 relev.), characterized by A. nemorosa and P. multiflorum and the absence of L. galeobdolon is partially similar to the former cluster 6; cluster 5 (15 relev.), with A.nemorosa resembles the former clusters 6 (partially) and 4; finally, cluster 6 (8relev.) and 7 (34 relev.) have characters as the former clusters 5 and 7 respectively.

As a consequence, the two stopping rules are very similar in the identification of the clear-cut, the N- and SW-corners, the SE-borders of forest and clear-cut and two interior parts (centred around the relevés nrs. 8 and 84 respectively) of the forest. However, the wet W-corner + brooklet and the NE-border are best outlined by stopping rule 1% and the southern forest-border by 5%. As a whole the two pictures are only slightly different.

In the next step, the commonest and the rarest taxa are eliminated so that only species with a presence between 5 and 95% are involved which reduces their number from 58 to 26 ; the splitting up of groups is carried out with the highest value of $\Sigma|V|$ and both stopping rules are applied. In the case of 5% six relevés cannot be clustered, in the case of 1% the "clear-cut" cluster is enlarged by additioning of relevés from its direct neighbourhood, the pic-nic sites and the NE-corner. Compared to the pictures in which all taxa were used the 1%-ones differ in a somewhat greater but not so considerable extent, the same conclusion applies to the sub-dividing species.

When using, as last step, the highest value of $\Sigma\ \chi^2$ in the sorting procedure, but retaining the 26 taxa and both stopping rules, the results are quite identical to those of the previous steps described.

3.1.3. Information analysis (IA)

Using the taxa to cluster the relevés the qualitative analysis (Figs. 3 and 5) reveals the existence of four clusters, already found by previous analyses. The clear-cut (cluster 1, extended to 20 relevés) reflects the most species-poor vegetation of the forest and is characterized by the (nearly) total absence of taxa like Anemone nemorosa, Lamium galeobdolon and Polygonatum multiflorum and the (not-overall) presence of Carex pilulifera. The soutern forest-border (cluster 2 with 32 relevés) is distinguished by a rather strong presence of Athyrium filix-femina, and the complete absence of Lonicera periclymenum; the wet W-corner (cluster 3 with only 6 relevés) by Paris quadrifolia and Primula elatior and the forest-part vegetation (cluster 6 with 13 relevés, by far the most species-rich one) by e.g. Stellaria holostea, Heracleum sphondylium, Poa compressa and Urtica dioica. The remaining two clusters (4 and 5, each with 22 relevés) represent the W- and E-part of the forest but are very poorly characterized, namely by Endymion non-scriptus and Blechnum spicant (pretty well confined to the W-part) respectively. However, the quantitative analysis is just capable to detect: firstly the clear-cut (reduced to 7 relevés) with the highest cover-values for Pteridium aquilinum, and secondly the wet W-corner (6relevés) with a lower cover of Anemone nemorosa and a higher cover of Ranunculus ficaria (as compared to the reduced cluster of 7 relevés which is confined to the vegetation-type of some forest paths).

Using the structural characters quantitatively (Fig. 4) the vegetation of clear-cut, wet W-corner and some forest-paths reappears clearly. In the former the upper herb layer displays a cover of usually 35% and the lower one a cover from 1 to 3% usually; in the latter the cover of the lower herb layer fluctuates from 60 to 85%, this of the upper one is insignificant. A third cluster reflects a vegetation-type which is mainly developed in the SW-corner and along the SE-forest border: both the upper and the lower herb layer are very poorly developed. The relevés of the remaining three clusters are very dispersed i.e. they are not restricted to well-defined areas in the forest.

In contrast to the result of the two normal information analyses discussed above, the clustering of taxa or the inverse information analysis produced no ecologically meaningful groups.

3.1.4. Orloci's sum of squares clustering technique.

When accounting for all species in order to define as well as possible the different vegetation-areas in the forest (Figs. 6 and 8), a surprisingly clear picture of the relevés has been obtained, reflected by eight clusters: cluster 1 (7relev.) with on the average the highest cover-values of Hedera helix and a regular presence of Blechnum spicant; cluster 2 (8 relev.) wherein Pteridium aquilinum is totally absent; cluster 3 (10 relev.) with cover-values of Holcus mollis regularly ≥ 5%; cluster 4 with a much higher presence-degree of Anemone nemorosa, Hedera helix and Sorbus aucuparia and on the average a remarkably higher cover of Rubus spec. (unlike cluster 5); cluster 6 (11 relev.) where P.aquilinum regularly shows cover-values of 15 and 35%, Acer pseudoplatanus is totally absent and Carex pilulifera occurs four times out of seven over the whole forest; cluster 7 (25 relev.) where Anemone nemorosa is always present and regularly shows values of ≥ 15% and to which species like Arum maculatum, Poa compressa and Primula elatior are very strictly limited; cluster 8 (23 relev.) with no specificity. Generally speaking, the picture is giving a series of well-defined homogeneous vegetation-types, except in the middle of the forest. Assuming that no more than 10 clusters would be distinguished in this technique, Beale's formula recommends two clusters as optimal number, but Hogeweg's formula ten.

The picture given by the clustering of structure-relevés is, once more, rather confused, i.e. not any cluster is spatially very restricted. Cluster 3 e.g. has a lower herb layer with a cover usually below 3% and an upper herb layer with cover usually 15 to 35%; this time cluster 3 is not restricted to the clear-cut. Cluster 2 (48 relev.) wherein both lower and upper herb layer shows a cover of maximally 5%, is dispersed over the whole forest but the N- and the NE-corner are remarkably well separated. Comparing the results of the two optimality formulas, the difference is more realistic: they confirm the existence of 5 and 7 clusters respectively.

Customarily, the clustering of taxa has given a meagre result, although the forming of the first groups occurred already at the similarity-level of about 55%.

3.2. Ordination techniques.

3.2.1. Polar ordination (Bray & Curtis) modified by Beals (POB)

In ordinating the vegetation-relevés using species, it is quite clear that distinguishing groups as in the preceding classification methods is impossible. Moreover, the distribution of relevés along the X-axis is unilaterally shifted so that a correlation with some gradient cannot be expected. Along the Y-axis however, a structural gradient is appearing. The highest scored group (1) represents particularly species from the upper herb layer, i.e. Pteridium aquilinum and Rubus spec. where the former one is outstanding by both presence and cover. The central group (2) is especially characterized by taxa both from lower and upper herb layer, namely Hedera helix and Rubus spec. respectively, where the former is predominant. In the lower herb layer Anemone nemorosa and Polygonatum multiflorum mainly point out the lowest scored group (3) where the former one of course is giving by far the highest cover-values. Group (1) is obviously confined to the clear-cut and the dry N-corner, group (3) chiefly to the eastern part of the forest. The YZ- and ZX-configuration do not give any additional information.

Starting from structural characters six well-defined groups of relevés are formed. The affinities along the X-axis are obscured but the gradient is once more clear along the Y-axis: both cover and height of the upper herb layer are gradually changing viz.decreasing. The clear-cut and some relevés from the wet W-corner and the forest-paths are giving, on the average, high values when compared to the rest of the forest, whereas a group of relevés in the eastern part (between the picnic site and the brooklet), the dry northern part of the center and some relevés in the wet W-corner, do not have an upper herb layer at all. More information is not yielded by the configurations on the other axes.

Trying to distinguish groups of species seems to be speculative.

3.2.2. Simple ordination (SO)

In the I/II-configuration the grouping of relevés-based on the use of taxa- is clearly depicted along the abscis but rather obliquely. The gradient is largely dependent on species highly representative for an important structural character, i.e. the height of the herb layer. Group 1 (13 relev.; the wet W-corner and parts of some forest-paths) is typified by lower herb layer-species like Anemone nemorosa, Lamium galeobdolon, Ranunculus ficaria and in a lesser degree by Arum maculatum, Primula elatior and Poa compressa. The group at the other end of the gradient (5; 7 relev.) is particularly characterized by upper herb layer-species like Pteridium aquilinum and Rubus spec.; in this clear-cut vegetation P. aquilinum has by far the highest cover values. In going from both ends to the middle group (78 relevés respresenting a mixture of lower- and upper herb layer-taxa without any dominance), two groups are noted, one (8 relevés) where Anemone nemorosa and Lamium galeobdolon show a high presence degree but on the average low quantities, the other (3 relev.) with Rubus spec. as the most dominant taxon and much less frequent Pteridium aquilinum.

In the II/III-configuration the group of nine relevés is fully absorbed by the middle group but a sixth cluster (10 relv.) evolves from this middle group: in diminishing order are here Holcus mollis, Hedera helix and Oxalis acetosella the most representative taxa. This vegetation-type is nearly entirely restricted to the SE-corner of the forest. As a consequence, the general situation is represented best by the I/III-configuration (Fig. 9): the axis efficiency is, for I - II - III, 3.90, 0.21 and 14.75% respectively, which gives a total efficiency of 18.85 %.

These results are obtained from transformed data but without transformation the picture is very unsatisfying and difficult to interpret.

From transformed structural characters originate five rather well-defined relevés-clusters, of which four indicate a structural gradient along the abscis (I/II-configuration). Going from cluster 3 (the wet W-corner + some forest path-relevés) over cluster 4 (the least characterized part covering nearly half of the forest) and cluster 2 to cluster 1 (the clear-cut), the cover of the upper herb layer is on the average increasing, while this of the lower one is on the average decreasing. The fifth relevés-cluster is found along the high scored positive part of axis II; it totally lacks the upper herb layer and gives low to very low cover values in the lower one. Finally, seven quadrats with outstanding cover-combinations do not fit in any described cluster.

The efficiency of the axes I - II - III is 17.05, 74.71 and 0.03% respectively; the total efficiency is consequently 91.79%.

3.2.3. Optimized polar ordination (OPO)

Analyzing the quadrats on their species scores the first two axes (Fig. 10) account for nearly the same amount of variation, namely 21.12% and 21.84%, which is about twice the variation of the third axis (10.90%). The gradient is essentially characterized by Anemone nemorosa, whose cover is regularly decreasing from 35 - 60% (cluster 1) to 0 or 0.1% (clusters 5 and 6). Although six clusters are formed as such, only two can be readily detected in the field. Cluster 1 (10 relev.) where Anemone nemorosa depicts the highest cover percentages and where Arum maculatum and Poa compressa are very typical; this vegetation is again encountered in the wet W-corner and along some forest paths near the brooklet. Cluster 5 (15 relev.)- referring to the major part of the clear-cut and the SE-edge of the forest-includes either Pteridium aquilinum or Rubus spec. as predominant- both always present- and Carex pilulifera as very typical taxon. The distribution of the other groups is very heterogeneous.

When grouping structure-relevés, somewhat more variation is accounted for by axis I compared to axis II, namely 46.98 to 31.16%; 91.04 % is the total efficiency ratio of the three axes. Surprisingly, eleven clusters can be easily distinguished on the graph: axis I as well as axis II are clearly showing two structural gradients. On the former clusters 5 - 11 are situated: the UHL-cover remains very constant (0 or 0.1%) but the LHL-cover is steadily decreasing from 60 - 85% (cluster 1) to 0 - 0.1% (cluster 11). On the latter the four remaining clusters are found. While the LHL-cover is irregularly fluctuating between 0 and 85%, the UHL-cover gradually decreases from 35% to 1%. As such the maximal cover percentages are higher in the LHL. Very homogeneously are appearing the clear-cut (cluster 1) and the vegetation of the N-corner and east of it (about half of cluster 11), somewhat less clearly the wet W-corner and some forest-paths (cluster 5).

3.2.4. Position vectors ordination (PVO)

Using species to investigate the grouping af relevés in space, the coordinates for five axes are calculated. The efficiency ratios are 45.16%, 15.77% and 7.45% for the first, second and third axis respectively. There is obviously a tendency to more dense clustering towards the part of the first axis with the highest scores (Fig.11), due to a decreasing species diversity in the subsequent clusters, diminishing from an average of 12,4 species in cluster 1 to 5,7 in cluster 7. The gradient is again characterized by the gradually decreasing cover percentages of Anemone nemorosa: cluster 1 has values of 35 or 60 %, with typical companions like Arum maculatum and Poa compressa and rather typical ones like Primula elatior, Ranunculus ficaria and Heracleum sphondylium,while in cluster 5 Anemone nemorosa scarcely reaches 0,1% cover. In contrast to the second axis a gradient is reflected on the third axis also. Pteridium aquilinum, first absent or showing a very low cover (0.1%) and always dominated by the higher cover of Rubus spec. (up to 15%) which is always present, becomes gradually dominating (up to 35% whereas Rubus spec. never disappears). Clusters 5, 6 and 7 are nearly exclusively involved here. Thisanalysis results in the detection of the wet W-corner + some forest paths (cluster 1), the clear-cut + SE-edge of the forest (cluster 6), the NW-corner + N-edge of the clear-cut + part of the SE-corner (cluster 7).

The analysis of structural features provides the highest total of efficiency ratios, namely 94.73%: axis I accounts for 58.00%, axis II for 27.38% and axis III for 9.35%. The tendency to dense clustering in the high scored part of axis I (see also Orloci 1966) is more pronounced as compared to the quadrat-clustering. The gradient exposed along the axis I reflects a double one: from cluster 1 to 5 the LHL-cover is regularly decreasing while the UHL-cover constantly remains very low and from cluster 6 to 10 the UHL-cover at its turn is permanently diminishing combined with a very low or lacking LHL-cover. The second axis is reflecting a decreasing LHL-height from the high negative scores to the high positive ones. At any rate, the wet W-corner + some forest paths (cluster 1), the clear-cut (cluster 6), the N-corner (cluster 3) and the small corner east of it (cluster 10) are readily identified.

4. Comparison and discussion of the results of the different techniques.

4.1. Classification.

4.1.1. Relevés-grouping with taxa.

NAA, being the only divisive classification method used, gives more than sufficient results. Irrespective as to whether the total number of species is maintained or reduced and as to whether max $\Sigma|V|$ or max. ΣX^2 are chosen to increase the homogeneity-level of the quadrat-groups, with a stopping-rule of 5% or 1%, the same vegetation-types can be well delimited (cfr.3.1.2.). In practice however only five types can be retained because of their recognition in the field. There is one exception however: with all the taxa involved, max. $\Sigma|V|$ as the association parameter and 1% as stopping rule, the wet W-corner shows a higher degree of homogeneity and the quadrats along the brooklet are more distinctly separated in two clusters. That means that this NAA-variant results in six detectable vegetation-types. So we can agree with the opinion of Pritchard & Anderson (1971) in their study on heathland and grassland communities that NAA can effectively relate the groups to the sites. In both variants where all species are included in the analysis, some quadrats like nr. 107 are not classified.

Compared to NAA, normal IA (NIA) does reflect a rather different picture: e.g. not any relevé along the brooklet seems to be related to the wet W-corner, the N-corner falls apart in two clusters, the SW-corner has lost its identity while the clear-cut-cluster shows a great expansion with basically a negative characterization. Because we are obviously interested in the upper-level clusters of NAA and NIA, we can make Lambert & Williams' (1966) opinion nevertheless ours where they conclude that "association-analysis will probably serve his purpose almost as well as information-analysis". For very different vegetations Ivimey-Cook e.a. (1975) and Webb e.a. (1967) reached very similar conclusions. The use of quantitative multistate instead of binary characters is disappointing: it looks like this NIA-procedure should not be suitable for data which contains too much information (Orloci 1968).

Between the two remaining classification techniques, UPGC and MVC, the results are unquestionably in favour of the latter. MVC produces the greatest number of clusters recognizable in the forest. In contrast to Grigal & Goldstein (1971) no reversals are noted in our dendrogram (but see 4.1.2.

Finally, after comparison with the analyses making use of the information statistic, we have to agree with Burr (1970) when he is stating that Sum of Squares clustering can be preferred sometimes.

4.1.2. Relevés-grouping with structural characters.

Obviously this grouping with such a limited number of variables can only be quantitative. A small number of clusters can be located to certain sites in the forest, whereas the other ones are highly intermingled, as such creating a very heterogeneous picture; NIA is somewhat better than MVC and UPGC. The MVC-dendrogram is showing two reversals occurring in the lower-level groupings.

4.1.3. The optimal number of clusters.

Authors like Bottomley (1971) and Orloci (1970) have thoroughly discussed the unsuitability of using the one-tailed χ^2-distribution as a significance test, as proposed by Field (1969), e.g. because postulating a reasonable null hypothesis for subsequent tests is impossible. For this reason, we had to recourse to the formulas of Beale and Hogeweg. Up till now the former has been more often applied (Van Hecke e.a., 1976); consequently we may conclude with caution that the latter is giving less satisfaction.

4.2. Ordination

Although the first aim of ordination is to relate the quadrats in space to certain gradients located on the (orthogonal)axes, attention will also be paid to the number of vegetation-types which can be detected.

4.2.1. Relevés-ordination with taxa.

Undoubtedly, POB produces the least satisfying results: only one cluster is distinct and one height-gradient on the Y-axis. From the other three ordination techniques, a smaller number of clusters - identifiable in the field - can be extracted as compared to the classification procedures.

Moreover, SO an OPO are able to discover a height- and a cover-gradient respectively on the first and second axis only, PVO however shows a cover-gradient both on the first and third axes. Furthermore, the total variation, extracted for the first three axes in PVO and OPO, accounts for four resp. three times that in SO. Therefore, our findings concerning the analyses SO, OPO and PVO completely confirm Orloci's (1966) conclusion that gradients are more and more obscured with declining the efficiency ratios. Similarly as in his study, the first axis in SO does not necessarily extract the greatest amount of variation. This is particularly due to the fact that the choice of the axes is based on reference stands instead of on their relative importances, which inevitably results in a loss of ordination efficiency: the axes do not coincide with the direction of maximal variation (Austin & Orloci 1966). We agree with the opinion of Noy-Meir (1977) that the direction of the axes through the point space differs very slightly between OPO and PVO; whereas both methods maximize the same criterion, namely the sum of squared projections, the additional constraint which requires axes to pass through one (or two points) has little influence. Still more explicit as in SO, as stated by Bannister (1968), species-rich quadrats show greater interstand distances as species-poor ones (with only species of very low cover-abundance) in the first two-axes configurations of the OPO- and PVO-methods.

4.2.2. Relevés-ordination with structural characters.

While the POB-technique is giving three sharply defined field-clusters, the other three are not much more successful and produce only four and invariably the same well identifiable vegetation-types. In addition, in the SO- ordination seven quadrats are isolated, more or less grouped but without close relationship.

In detecting structural gradients, the results of POB and SO are very similar, except for the axes (Y-axis in BOP, first axis in SO). Although the total percent extraction value for the first three axes in the OPO- and PVO techniques are very high and only very slightly different, the results are not quite similar: while OPO can distinguish a cover-gradient on axes I and II, PVO is showing a double cover-gradient on the first and a height-gradient on the second axis. Consequently, PVO produces better results as was the case in the ordination with taxa.

5. Comparison of the spring and summer forest.

Because in spring very few trees or shrubs have leaves, only the taxa of both herb layers are involved. In summer, the shrub and the only herb layer are dealt with jointly (Van Hecke e.a. 1976). Consequently, spring and summer data are partially comparable. Moreover, merely the UPGC- and NAA-methods are applied in both studies.

While for the UPGC-technique the summer forest exhibits four well identifiable vegetation-types in the field, namely (1) certain forest paths, (2) the wet W-corner, (3) the dry N-corner and (4) the clear-cut, only vegetation-type (3) and parts of (1) cannot be recovered in the spring forest (Fig. 7). This is not surprising for vegetation-type (3), for it is neither in summer nor in spring characterized by taxa from the herb layer. The parts of (1) are directly related to the vegetation of the wet W-corner, but the relevés nrs. 12, 24, 58, 65, 68, 81 and 83 have disappeared since they do not show any typical spring-taxon of high cover-abundance. In this way, the spring forest seems less differentiated as compared to the summer forest.

The reverse seems to be true when applying NAA, as well with the 5%- as with the 1%-stopping rule. Besides the clear-cut, the spring-picture of 5% (Fig.1) still shows the SW-corner + the western E-part, the SE-border of the clear-cut, the dry N-corner + the SE-forest-border, the two forest-parts around the quadrats nrs. 84 and 8. The 1% (Fig. 2) picture reflects clearly besides the clear-cut, the wet W-corner, the dry N-corner, and the SW-corner, also vegetations from the two forest-parts around the quadrats nrs. 84 and 8, the SE-corner and the NE-forest-border.

Summary

From 115 quadrats, laid out in the same way and on the same coordinates as described in a first paper, cover-abundance and height data were collected in april 1978 on 58 taxa, belonging to the upper and lower herb layer, on the moss layer as a whole and on the litter. They were submitted to four classification methods, namely Unweighted pair-group centroid technique (UPGC), normal Association analysis (NAA), agglomerative normal and inverse Information analysis (NIA and IIA), Minimum variance clustering (MVC), and to four ordination methods, namely Beals' Polar ordination (POB), Simple ordination (SO), Optimized polar ordination (OPO) and Position vectors ordination (PVO).

The only divisive method (NAA) produces more than sufficient results: they are slightly better with the 1%-stopping rule especially when no species reduction is involved. NAA and NIA give quite similar results. From the three agglomerative techniques, the greatest number of vegetation-clusters (7), recognizable in the field, has been obtained with MVC, the poorest picture however by UPGC. With regard to the forest-structure, the better results are with NIA, followed by MVC. Moreover, NIA applied in a quantitative way, is less appropriate. The outcome of species classification is not interpretable.

The ordination results obtained by OPO and PVO are unmistakably better as compared to those from POB and SO, as well in discovering gradients as clusters; the gradients particularly reflect changes in cover-abundance and height. In the ordination of vegetation-quadrats, the total of the efficiency ratios extracted for the first three axes in PVO and OPO are respectively four and three times higher than with SO. Concerning the structure-quadrats, the percentage extraction values are very high and very alike.

Comparing the spring- with the summer-forest, UPGC distinguishes more identifiable vegetation-types in the summer data, NAA on the contrary in th spring data.

Samenvatting

In april 1976 werden op dezelfde plaatsen als in 1974 (Van Hecke et al., 1976) opnieuw 115 proefvlakken uitgelegd. Bedekking en hoogte werden bepaald op de hogere en lagere kruidlaag, de mos- en strooisellaag; 58 Phanerogamen werden ontmoet. Naast de struktuur werd ook de vegetatiesamenstelling geanalyseerd m.b.v. vier klassifikatie- en vier ordinatietechnieken.

Vergeleken met de agglomeratieve normale Informatieanalyse (NIA) verschaft de (divisieve)normale Associatieanalyse (NAA) evengoede resultaten; opnieuw levert in NAA de haltdrempel van 1% wat duidelijker groepen op als die van 5%.

Vergeleken met de overige beide agglomeratieve technieken, nl. "Unweighted pair-group centroid method (UPGC)" en "Orloci's Sum of Squares clustering technique" of "Minimum variance clustering" (MVC), neemt NIA een middenpositie in voor de opbouw van het vegetatiebeeld; MVC levert het grootste aantal in-het-veld-herkenbare clusters. Betreffende de bosstruktuur haalt NIA het op MVC. Toegepast op een kwantitatieve manier is NIA minder geschikt.

Ontegensprekelijk geven "Optimized Polar Ordination" (OPO) en "Position Vectors Ordination"(PVO) betere resultaten dan "Beals' Polar Ordination" (POB) en "Simple Ordination" (SO). In de ordinatie van vegetatieopnamen ligt de variantie, vastgelegd op de eerste drie assen, 4 x respektievelijk 3 x hoger in PVO en OPO als in SO; voor de struktuuropnamen liggen de drie variantiewaarden veel hoger maar verschillen onderling zeer weinig.

Voor de analyse van de zomervegetaties is UPGC geschikter dan NAA, maar het omgekeerde is waar voor de lentegegevens.

Résumé

Cent quinze quadrats ont été systématiquement espacés en avril 1976 aux mêmes endroits de la fôret qu'en 1974 (Van Hecke et al., 1976). Des données, relatives au recouvrement et à la hauteur, ont été récoltées sur 58 Phanérogames dans les deux strates herbacées, ainsi que dans les strates de bryophytes et de la litière. Nous avons analysé la composition végétale et la structure forestière à l'aide de quatre méthodes de classification et de quatre méthodes d'ordination.

Les résultats, obtenus par l'analyse normale des associations interspécifiques (NAA) et par celle de l'information agglomérative (NIA), sont très bien comparables; de nouveau la délimitation des groupes chez NAA est un peu mieux au seuil de 1% qu'à celle de 5%.

Comparée à deux autres techniques agglomératives, notamment "Unweighted pair-group centroid method" (UPGC) et "Orloci's Sum of Squares clustering technique" ou "Minimum variance clustering" (MVC), NIA occupe une position intermédiaire en ce qui concerne la classification des relevés; MVC produit le plus grand nombre d'unités de végétation reconnaissables dans le terrain. Considérant la structure forestière, NIA est plus effective que MVC. Appliquée d'une façon quantitative NIA nous paraît moins valable.

Les résultats obtenus par "Optimized polar ordination" (OPO) et "Position vectors ordination" (PVO) sont incontestablement beaucoup mieux que ceux par "Beals' polar ordination" (POB) et "Simple ordination" (SO). En plaçant dans l'espace les relevés de végétation, la variance, extraite des premières trois axes de PVO et OPO, surpasse quatre respectivement trois fois celle de SO; effectuant l'ordination des relevés de structure, les trois valeurs de variance sont beaucoup plus grandes mais diffèrent entre eux fort peu.

En ce qui concerne les données estivales de 1974, l'analyse s'effectue mieux par UPGC que par WAA; en ce qui concerne les données printanières de 1976, on peut constater le contraire.

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Table 1. Taxa, found in the "Aalmoeseneiebos" (Gontrode: 50°49' N., 3°48' E.) in mid-April 1976, with their codenumbers.

Acer psnudoplatanus	0002	Humulus lupulus	0639
Adoxa moschatellina	0010	Juncus effucus	0680
Aegopodium podagraria	0011	Lamium galeobdolon	0702
Agrimonia eupatoria	0013	Lonicera periclymenum	0759
Agrostis canina	0018	Luzula pilosa	0770
Ajuga reptans	0024	Lysimachia vulgaris	0784
Anemona nemorosa	0056	Maianthemum bifolium	0786
Anthriscus sylvestris	0070	Ornithogalum umbellatum	0805
Arctium minus	0084	Oxalis acetosella	0909
Arrhenaterum elatius	0096	Paris quadrifolia	0920
Arum maculatum	0103	Poa annua	0952
Athyrium filix-femina	0119	Poa compressa	0955
Blechnum spicant	0146	Poa trivialis	0959
Caltha palustris	0187	Polygonatum multiflorum	0964
Cardamine pratensis	0205	Primula elatior	1014
Carex pilulifera	0251	Pteridium aquilinum	1022
Carex remota	0258	Pyrola rotundifolia	1034
Carex strigosa	0263	Ranunculus ficaria	1047
Carex sylvatica	0264	Ranunculus repens	1056
Corylus avellana	0366	Rumex obtusifolius	1101
Deschampsia cespitosa	0397	Sambucus nigra	1133
Dryopteris dilatata	0419	Endymion non-scriptus	1151
Dryopteris carthusiana	0426	Sorbus aucuparia	1227
Filipendula ulmaria	0526	Stachys sylvatica	1246
Galium aparine	0546	Stellaria holostea	1249
Glechoma hederacea	0582	Teucrium scorodonia	1273
Hedera helix	0598	Urtica dioica	1321
Heracleum sphondylium	0607	Vinca minor	1377
Holcus mollis	0632	Rubus spec.	1402

Fig. 1. Normal Association analysis (NAA): distribution of vegetation-relevés. Subdivision at the probability level of 5%.
Cluster symbols: ⊖ = cluster 1, ◒ = cluster 2, ■ = cluster 3, ⊗ = cluster 4, ◉ = cluster 5, ▲ = cluster 6, ⨂ = cluster 7, □ = cluster 8.

Fig. 2. Like Fig. 1, but at the probability level of 1%.

Fig. 3. Normal Information analysis (NIA): distribution of vegetation-relevés, using the presence - absence scores of taxa. Cluster symbols: see Fig. 1.

Fig. 4. Normal Information analysis (NIA): distribution of structure-relevés, using the structural characters quantitatively.
Cluster symbols: see Fig. 1.

Fig. 5. Normal Information analysis (NIA): dendrogram of vegetation-relevés. Dashed line: level on Fig. 3. Number-row: number of vegetation-relevés.

Fig. 6. Minimum variance clustering (MVC): dendrogram of vegetation-relevés. Dashed line: level on Fig. 8. See further Fig. 5.

Fig. 7. Unweighted pair-group centroid method (UPGC): distribution of vegetation-relevés. Cluster symbols: see Fig. 1.

Fig. 8. Minimum variance clustering (MVC): distribution of vegetation-relevés. Cluster symbols: see Fig. 1.

Fig. 9. Simple ordination (SO; Perpendicular axes technique). Point space composed of vegetation-relevés, axes I and III.
* = replaces 48 relevés. Symbols: see Fig. 1.

Fig. 10. Optimized polar ordination (OPO): Point space composed of vegetation-relevés, axes I and II.
* = replaces 28 relevés. Symbols: see Fig. 1.

Fig. 11. Position vectors ordination (PVO): Point space composed of vegetation-relevés, axes I and II.
* = replaces 26 relevés. Symbols: see Fig. 1.

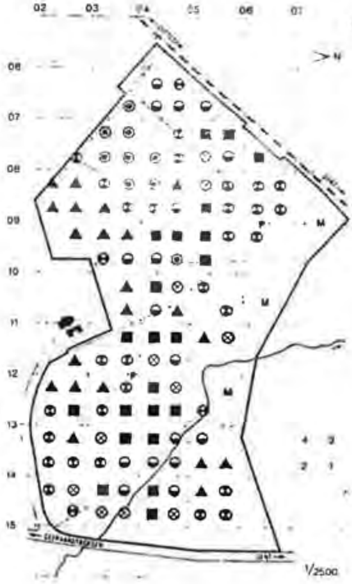

Fig. 1

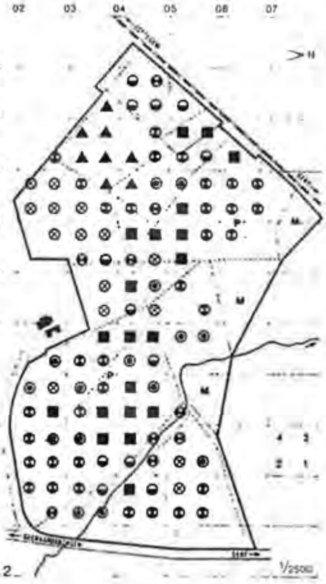

Fig. 2

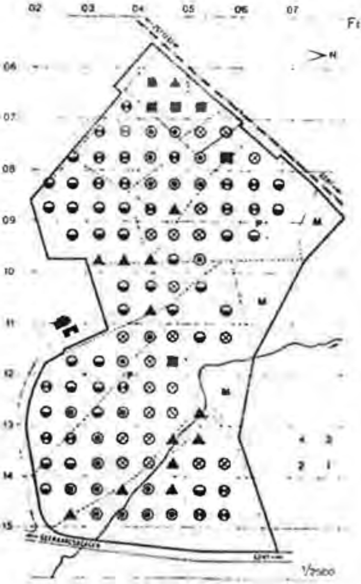

Fig. 3

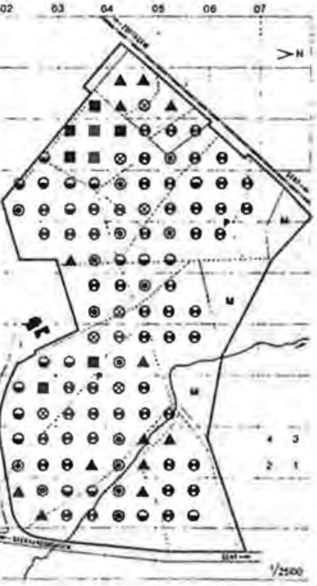

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Fig. 5

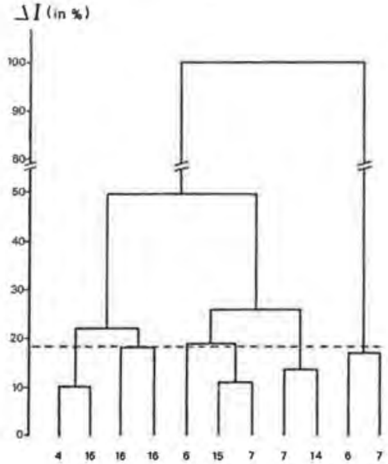
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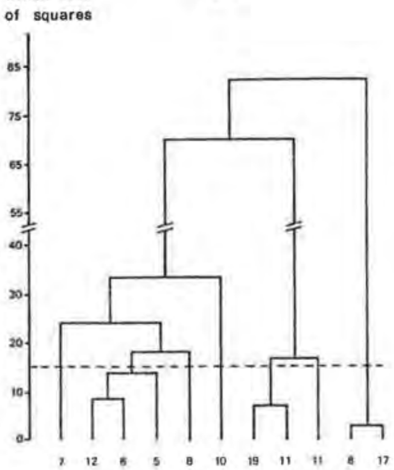
Fig. 6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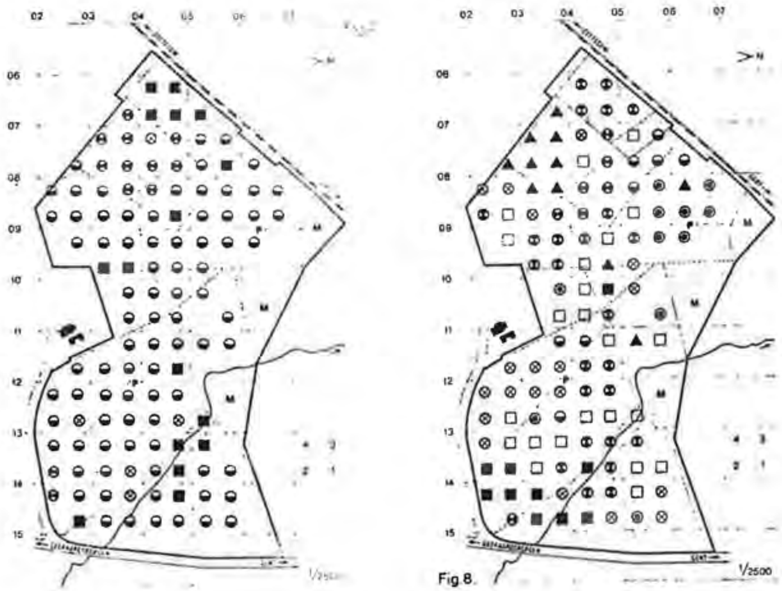
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Fig.8.

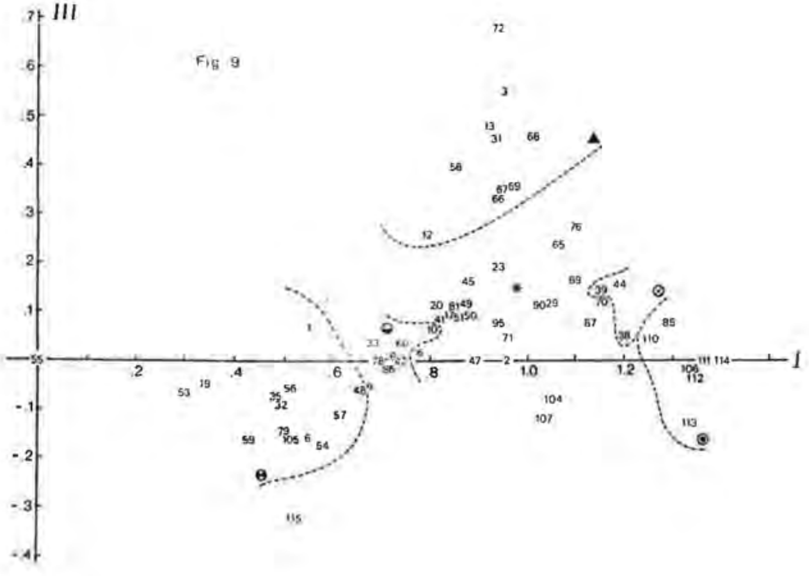
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Fig 9

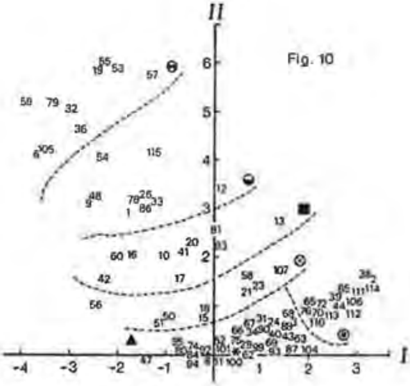

Fig. 10

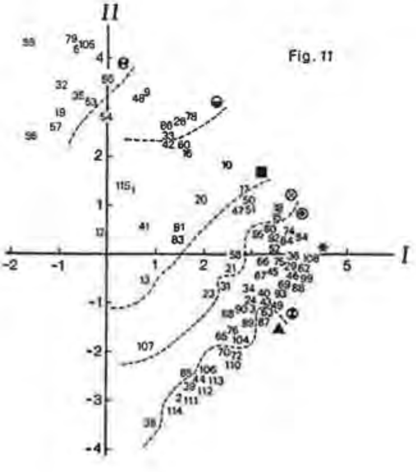

Fig. 11