

BE / ISSN 0587-1476

SYLVA GANDAVENSIS

1976

N°43

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

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Keywords :

Association-analysis, Belgium, Brabantine District, Cluster analysis,
Flemish District, Gontrode, Mixed forest, Multivariate analysis, Prin-
cipal component analysis.

Introduction

For years this forest has been permanently and intensively studied by
researchers and students from the State University of Agriculture in
Ghent (Belgium). Especially problems in forestry and much less in re-
creation were handled. As a result, only one study (Roskams, 1956 [†]),
dealt with some phytosociological aspects in the manner of the Zürich-
Montpellier School.

Therefore, the need was felt to analyse some vegetational aspects more
thoroughly and on a mathematical basis.

The aim of this paper is to handle the data collected in summer. Those
gathered in spring and other data related more to diversity and pattern,
will be treated in later papers.

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

** We are much indebted to Prof. dr. ir. M. Van Miegroet for permission
to work in this forest, to Prof. dr. ir. R. Goossens for technical
assistance, and to Dr. P. Hogeweg (Utrecht).

[†] "Toepassing van de bosbouwkundige detailplanning op het bos te
Gontrode". Thesis, Rijkslandbouwhogeschool Gent, 83 pp.

Study area and sampling methods

The "Aelmoeseneiebos" forest (50°49'N, 3°48'E) is situated on the territory of Controde and Landskouter (East Flanders) and has a total area of about 28 ha. Only the central part, with the railway Ghent - Zottegem as NW-border and the road Ghent - Geeraardsbergen as E-border, was used as study area (about 19 ha). It shows a gradually slope from the S (22 m) to the N (12 m). Historical sources mention its existence for the first time in the 9th century. Presumably, the site was never totally deforested in the following centuries, although the tree layers in particular were permanently managed.

The forest can be situated in the transition zone from sandy to loamy soils ; the following soil types were recorded : Lcc, slcc, ldc, wldc, (w)ldc, Lhc, wLcp and Ldp (Leys, 1966). The two phytogeographical districts mentioned in the title are the Flemish and the Brabantine district respectively (De Langhe et al., 1973).

During August and September 1974 two of us (T.V.T. and V.V.) laid systematically out 115 quadrats of 20m x 20m. Formerly, a screen of numbered wooden pickets was placed over the whole area ; the distance between two pickets in this "regular" distribution was about 70 m. Each screenquadrat usually contained four relevé-quadrats, except at the edges of the forest. Each relevé-quadrat got a number derived from the coordinate-numbers on the nearest picket, and an additional number (from 1 to 4) referring to its quarter position (Tab. 1 and Fig. 1).

For each relevé were recorded : 1) the real cover (Barkman et al., 1964) of all vascular species (122 taxa : Tab. 2) and of the bryophytes (handled as a group of species) on the altered Braun-Blanquet scale (- 1 %, 1 %, 3 %, 5 %, 15 %, 35 %, 60 % and 85 %).

2) the layers in which they were represented : first (dominant) and second tree layer, shrub, herb and moss layer.

3) the total cover and height of each layer.

4) the height of the litter.

Following the Flora-list of Van der Maarel each taxon was characterized with a code-number for computer analysis ; only a few taxa got a new number.

Classification and ordination techniques

1. Cluster analysis

1.1. Hierarchical grouping method (HG).

Ward (1963) developed this method to optimize an objective function, which can be chosen arbitrarily and which is the sum of the within group error sum of squares :

$$e^2 = \sum_{j=1}^n \sum_{k=1}^m (x_{jk} - \bar{x}_k)^2 \quad (1; \text{Adam et al., 1975})$$

where n is the number of quadrats in a cluster, m the number of taxa and \bar{x}_k the mean value of taxon k in this cluster.

This happens at any clustering level while grouping t clusters of relevés or taxa into $k < t$ clusters of relevés or taxa at any one stage. This clustering criterion has been calculated iteratively using the method of Wishart (1969).

Properties of the method have been discussed by Hogeweg (1976) and Van Schaik and Hogeweg (1977). These include the tendency to group objects which have little resemblance to all other objects although they are mutually not very similar either. A special case of this property is the tendency noted by Adam et al. (1975) to group rare species, which can be inconvenient. However the most important feature of this clustering technique is its high discrimination power, which is very valuable in classificatory work in vegetation analysis. This last feature has also been assessed by Frenkel and Harrison (1974).

Grouping the taxa, the original data were logarithmized and the association between them computed by the Phi-coefficient of Pearson (Dagnélie, 1975) :

$$\varphi_{ij} = \frac{n \cdot n_{ij} - n_{ii} n_{jj}}{\sqrt{n_{ii} \cdot n_{jj} (n - n_{ii}) (n - n_{jj})}} \quad (2)$$

where n_{ii} is the number of relevés with only the i th species, n_{jj} the number of relevés with only the j th species, n_{ij} the number of relevés with both species common and n the total number of relevés.

Grouping the vegetation-relevés, by means of the taxa or the structural characters, the distance between the logarithmized original data was measured by the Mean Square Distance or Euclidean Distance (Sneath & Sokal, 1973) :

$$\Delta_{jk} = \left[\sum_{i=1}^n (x_{ij} - x_{ik})^2 \right]^{1/2} \quad (3)$$

and the average distance

$$d_{jk} = \sqrt{\Delta_{jk}^2/n} \quad (4)$$

where x_{ij} and x_{ik} are the values of the i th taxon or structural character in the vegetation-relevés j and k .

Grouping the structure-relevés by means of the structural characters or taxa, the difference between the standardized original data was measured with the Mean Character Difference (Sneath & Sokal, 1973) :

$$\frac{1}{n} \sum_{i=1}^n |x_{ij} - x_{ik}| \quad (5)$$

where x_{ij} and x_{ik} are the values of the i th structural character or taxon in the structure-relevés j and k .

1.2. Unweighted pair-group centroid method (UPGC).

Instead of the squared Euclidean distance, recommended by Lance & Williams (1967), Jaccard's similarity-index as modified by Spatz (Mueller - Dombois & Ellenberg, 1974) was used :

$$IS_{SP} = \frac{\Sigma(M_w : M_g)}{a + b + c} \times \frac{M_c}{M_a + M_b + M_c} \times 100 \quad (6)$$

where a , b and c are the number of species unique to relevé A, unique to relevé B and common to relevés A and B respectively ; M_a , M_b and M_c are the sum of quantitative values of the species unique to relevé A, unique to relevé B and common to relevés A and B ; M_w and M_g are the smaller respectively the greater quantitative values of a species common to relevés A and B. The procedure is described in detail in Spatz & Siegmund (1973).

The non-metric formula is applied to the classification or grouping of taxa, relevés and structural characters.

Despite the artificial nature of the centroid or "average" relevé (Beals, 1973) this clustering technique has the theoretical advantage that the groups or clusters grow in information content as analysis proceeds and becomes progressively less sensitive to errors and accidents in the data (Williams, Lambert & Lance, 1966).

To determine the number of clusters, the formula of Beale (Kendall, 1972; Everitt, 1974) is incorporated in the programmes of these two clustering methods :

$$F(c, c_1) = \frac{R_{c_1} - R_c}{R_c} \left\{ \frac{n - c_1}{n - c} \left(\frac{c}{c_1} \right)^{2/p} - 1 \right\} \quad (7)$$

where F is a pseudo-F-value, c the fixed maximal number of clusters, c_1 the presumed optimal number of clusters, R_c and R_{c_1} the sum of deviations from c respectively c_1 cluster centres, n the number of relevés and p the number of taxa.

This results in a triangular matrix of optimality values.

2. Association analysis (NAA).

The normal or Q-mode analysis was applied to those taxa with a constancy degree between 8 and 92 %, i.e. 44 instead of 122. The chi-square as well as the point correlation coefficient V were computed ; the first with Yates' correction, the second as :

$$V = \frac{ad - bc}{[(a + b)(a + c)(b + d)(c + d)]^{1/2}} \quad \begin{array}{l} = \text{index of} \\ \text{association} \\ \text{(8; Poole,} \\ \text{1974).} \end{array}$$

The computation of each association matrix was continued until none of the single chi-square values exceeded a certain probability level. As scale of classification the highest ΣX^2 was used. The splitting up of the groups of relevés was carried out with the highest $\Sigma |V|$, combined with a probability level of 1 % ($X^2 = 6,64$) or 5 % ($X^2 = 3,84$).

3. Principal component analysis (centered PCA).

Carried out in R-mode, matrices of covariances and correlation coefficients were computed from logarithmized data. Only for the first five components the eigenvalues and eigenvectors were calculated, using the Hotelling iteration method but in general only three of them will be discussed.

For the computation of the correlation matrix, Pearson's product moment correlation coefficient was used :

$$r = \frac{\sum_{i=1}^n (x_i - \bar{x})(y_i - \bar{y})}{\left[\sum_{i=1}^n (x_i - \bar{x})^2 \sum_{i=1}^n (y_i - \bar{y})^2 \right]^{1/2}} \quad (9)$$

(Conover, 1971)

where x_i and y_i are the values of the variates (or items) x and y in the i th item (or variate) whilst \bar{x} and \bar{y} are the means.

This pure mathematical ordination technique was recently criticized by Beals (1973) because rigid mathematical formality is combined with ecological casualness and because a species (in a species-dimensional space) is considered as an orthogonal component of ecological distance instead of an ecological variable in the vegetational space. Consequently, the curvilinear distortion can be fierce (Bouxin, 1976).

Techniques 1.1 and 3 were part of the NUMTAX Sequence, a subset of BIOPAT program system for biological pattern analysis, written by P. Hogeweg & B. Hesper (1972 ; Theoretical Biology, State University Utrecht)*.

P. Hogeweg kindly put this program, implemented on the IBM 370-165 of the Technical University of Delft at our disposition.

Programs for the methods 1.2 and 2 are written by ir. L. Bamps (U.I.A.), the computations were carried out on the PDP 11/45 computer of the Universitaire Instelling Antwerpen.

All techniques were applied to two different data-sets : on the one hand the four layers with the vascular plants, on the other hand the shrub and herb layers alone. This was done with the idea to eliminate largely anthropogenic influences on the data since tree species especially have been managed through planting and thinning techniques.

Comparison of the results within each technique

1. Cluster analysis

1.1. Hierarchical grouping method

To perform the taxa-clusters of the forest as a whole, only the species with a presence between 4 and 95 % were used, irrespective of the number of layers in which they occurred. Consequently, their number was reduced from 122 to 63. Considering the shrub and herb layer only, no reduction in degree of presence was involved, but a species occurring in both layers was handled as being two species. The floristic reduction due to

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the eliminating of both tree layers was amazingly very slight : only *Salix alba* (1116), and *Populus nigra* (2005) disappeared. As a consequence, the α -diversities in both approaches differ hardly.

As a whole, with rather low similarities - especially when all the strata are taken into account - the final result of the clustering is disappointing : the clusters are either too small or too large. In other words, the tendency to form specific combinations or vegetation types is only very slight.

Using taxa, the clustering of vegetation-relevés happens in the four as well as in the two lower layers at high similarity levels (Figs. 2a and 2b). Comparing Fig. 3a and 3b there is rather considerable overlap between some clusters.

Taking Fig. 3a as a reference-figure, this Hierarchical Grouping Method regularly reveals the existence of four distinct vegetation-types, when considering the entire forest or the shrub and herb layer alone : clusters 1 (along the brooklet), 2 (the wet W-corner), 5 (the clear-cut) and parts of 6 (the SE-edges of the clear-cut and the forest and the NE-corner). The sites occupied by cluster 6 are floristically more consistent in the tree layers, but display a smaller variety in their shrub and herb layer.

Taking now Fig. 3b as a reference-figure and only taking into account the shrub and herb layer, one cluster consisting of 5 relevés is added : those surrounding relevé 28 (N-corner) which behave very independently and form a *Pteridium-Sorbus - Prunus serotina* vegetation with low cover-percentages in shrub and herb layer. Clusters 2, 4 and 5 on the contrary show a greater floristic consistency in their shrub and herb layer, but a greater variety in the tree layers.

A smaller cluster in the center of the forest (consisting of relevés 9, 10, 60 and 78) is always present but rather latent : it fits in with cluster 3 (Fig. 3a : all the four layers), or with cluster 2 (Fig. 3b : the two lower layers only).

The clustering of vegetation-relevés with the aid of structural characters gives an only slightly different picture.

Grouping the structure-relevés by means of structural characters (Fig. 4a) or taxa (Fig. 4b) reveals a great similarity, except for the cluster 4 in Fig. 4b which cannot be characterized.

Moreover, the appearance of the four distinct vegetation types (Fig. 3a) is somewhat disturbed in the clustering of the structure-relevés. It must be remembered that both these clusterings are applied only to the four forest layers-data.

1.2. Unweighted pair-group centroid method.

The same precautions as in 1.1 for the taxa-clusters were taken, except that when considering the shrub and herb layer alone, a species occurring in both layers was treated as one species.

Again the similarities between the species are low to very low i. e. in general less than 30 %. Especially in the clustering of shrub and herb layer, the identification of all clusters is not easy and partially impossible, so that 32,5 % of the taxa remain unclustered.

Comparing Figs. 5a and 5b, where the vegetation-relevés are grouped according to the taxa, only the clusters 4 and 5 show a rather high conformity. The most remarkable fact is that cluster 1 of Fig. 5a is split up over three separate clusters (1, 2 and 3 in Fig. 5b) : cluster 1 refers to relevés along certain forest-paths where species are found which indicate the presence of ruderal and nitrogenous soils (in some cases rubble deposition). The parts of clusters 2 and 3 are entirely related to the corresponding parts of clusters 2 and 3 in Fig. 5a : again they reflect the humid to wet W-corner and the much drier N-corner typified by *Prunus serotina*. The two Figs. show a considerable resemblance except for the vegetation-cluster(s) along the brooklet, where the tree layers are very equal but not the shrub and herb layer.

Once more the picture given by the clustering of vegetation-relevés using structural characters is confusing. The clear-cut and its neighbouring wet W-corner (the *Populus - Primula* vegetation) only are found in both approaches. Obviously when treating all four layers, the tree layers are totally dominant.

This method reveals, in both approaches, the existence of the clear-cut and the W-corner, and, when using the taxa only, also the *Prunus* vege-

tation in the N-corner. A conform vegetation-cluster along the brook-let is appearing only when the four layers are considered. The two lower layers reveal the existence of a forest-path vegetation of human origin.

2. Normal association analysis

Dealing with the four layers as a whole, we get grosso modo the same results in applying either a 5 % stopping rule or a 1 % one (Figs. 5a and 5b). A very small number of relevés is then moving either between clusters 4, 5 and 6 or between clusters 2 and 3 (Figs. 7a and 7b). The vegetation of the clear-cut, the humid-wet W-corner and the ruderal forest-paths (clusters 1) is well defined. The N-corner (clusters 6) is now related to three relevés in the forest-center and five along the SE-edge. Moreover, the representative clusters are negatively characterized, that means identifiable only by the absence of species. When the max. χ^2 -level is lowered, namely to 48,60 and 41,62 resp. it seems that in about 2/3 of both clusters *Hedera helix* occurs. In both cases the relevés wherein this species is absent are the same : nrs. 29, 96, 99 and 101 ; they form largely the cluster of the forest-center.

The picture displayed by the two Figs. (8a and 8b) of the shrub and herb layer is more disturbed. The clear-cut, the humid-wet W-corner and the ruderal forest-paths again are easily detected. The N-corner together with the SE-forest edge are only persisting when the stopping rule of 1 % is handled ; but with 5 % they are absorbed in the much greater cluster 6 (Fig. 8a). For this reason and because the clusters 4 and 7 (Fig. 8b) are more clearly separated, the use of the 1 %-stopping rule gives a better result. Inevitably, two clusters are characterized by the absence of species at the level chosen ; but cluster 7 (Fig. 8a) possesses *Acer pseudoplatanus* in 19 of the 21 relevés, while cluster 6 (Fig. 8b) *Hedera helix* again in 10 of the 13 relevés.

To perform a normal analysis with structural characters instead of taxa is unnecessary and moreover much less informative (Fig. 8 c shows only one cluster which is comparable to one of the previous Figs. : the clear-cut).

As a conclusion this association-analysis is able to detect again the vegetation-types of the clear-cut, the humid W-corner and the ruderal somewhat nitrogenous soils along some forest paths. Defining the *Prunus serotina*-vegetation in the N-corner is rather faulty. It resem-

bles a small part of the forest-center (relevés nrs. 98, 99 and 101) and the SE-forest edge, except for one case where this vegetation-type disappears in a large cluster of 45 relevés (Fig. 8a : 6).

In addition to what is mentioned in the second paragraph the use of two stopping rules leads us to the conclusion that the 1 % stopping rule yields somewhat better results, which are easier for interpretation.

3. Principal Component Analysis

Starting from a variance-covariance matrix, comparing the results from four with those from two layers, and using the taxa - referring to 180 and 131 variates or floristic variables - an edaphic (hydrographic ?) curvilinear gradient can be detected as well on the first (accumulating 24 and 25 % respectively of the total variance) as on the third component (accumulating in both approaches 8 % of the total variance) : on the one end the taxa with high positive scores preferring not too dry crumbly soils and with not too deep ground-water table; on the other end the highly negative scored taxa preferring well drained and more compact soils. Moreover, a structural gradient has been found on the same components when considering the entire forest (i.e. four layers) : the highly negative scored taxa occur in less stratified and species-poorer parts compared with the highly positive scored taxa (Figs. 9a and 9b). Ordinating the relevés a clear hydrographic gradient is shown twice and only on the first eigenvector (Figs. 10a and 11a); but a structural gradient only once. The positive scored - higher than + 5 or + 3 respectively - relevés refer to places laying in depressions with insufficient drainage; the negative scored - higher than - 4 or - 1,5 respectively - relevés exhibit a low cover of the second tree and shrub layer. It means that more component axes are useful by ordinating the taxa, but the nature of the gradient seems to be more defined by ordinating relevés.

Restricted to the lower layers (shrub and herb l.), using the taxa and comparing now a variance-covariance matrix with one of correlation coefficients, the former matrix shows an edaphic (hydrographic ?) gradient again on the first and third component axes, the latter only on the first (Fig. 10b). This component accumulates only 9 % of the total variance. The positive scoring - higher than + 0,6 - taxa form the end of the gradient where the level of the soil water is high or rather high and displays distinct changes, whilst the negative scoring ones - higher than - 0,2 - characterize the well-drained part of this soil drainage gradient. Ordinating relevés the variance-covariance matrix reveals on the first

eigenvector a hydrographic gradient, the correlation matrix a structural one (Fig. 11b). Compared with the very remote relevé 54, the highest negatively scored relevés - more than $-0,5$ - show a tall shrub layer with intermediate cover, a rather low herb layer with low cover and a rather thick litter layer. This structural gradient appears also on the second eigenvector: the cover of the shrub and the height of the herb layer in the group of positively scored relevés - more than $+ 1,5$ - have twice respectively half of the corresponding layers in the group of negatively scored relevés - more than $- 0,75$. As a conclusion, here too the ordination of relevés gives more direct information. The nature of the gradients which are emphasized depend largely on the nature of the basic matrix.

Computing a matrix of correlation coefficients implies that e.g. the first five eigenvectors assimilate a much lower percentage of the total variance, compared with the computation of a variance-covariance matrix. As a result, more data - species or relevés - can be concentrated around the origin of the axes, so that only the extremes on the gradients are emphasized. This occurs when the relevés are ordinated but it does not hamper the detection and interpretation of the gradient(s) involved; on the contrary.

Comparison and discussion of the results of the different techniques.

Out of the three classification techniques (HG, UPGC and NAA), the last one is only able to demonstrate the existence of three well-defined independent clusters: the clear-cut, the humid-wet W-corner and the ruderal forest-paths. The remaining two (clustering) techniques reveal the existence of five clusters or vegetation-types. The HG-method shows besides the three vegetation-types just mentioned these of the N-corner, the SE-edges of the forest and the clear-cut and both sides of the brooklet. However, the UPGC-method exhibits the existence of the vegetation of the clear-cut, humid W-corner and the N-corner, but not of the edges of the clear-cut and the forest. Moreover, according to the use of the number of layers, this method detects the presence of both the vegetation along the brooklet and the ruderal forest-paths. Unlike the findings of Pritchard & Anderson (1971), NAA has in any case not helped to clarify the results of the clustering methods. Although both authors could compare five of these techniques instead of two, we can in general agree with them that HG produces generally the most attractive results. Moreover, more difficulties are met interpreting the UPGC-dendrograms as compared to the HG-dendrograms. In the former a variable number

of species, sometimes relevés, is clustered at very low similarity-levels. As a result, the dendrograms become very asymmetrical and the application of Beale's formula is practically impossible. Even a subjective stopping rule was hard to define by Pritchard & Anderson (1971). As a contrast with the study of Adam et al. (1975) taxon classification has in no way helped the interpretation of the relevé classification.

The occurrence of numerous reversals has enhanced the defining of clusters in the UPGC-dendrograms, whilst the phenomena of chaining and crowding were in a more or less degree always present. Williams et al. (1966) as well as Frenkel & Harrison (1974) have comprehensively discussed the nature of these problems ; they could demonstrate that the use of non-metric similarity coefficients gave the better results.

The power of the PCA to outline the clusters [vegetation-types] described above is much smaller. The clear-cut is always well shown, the vegetation on both sides of the brooklet rarely. Usually, its composition resembles that of the W-corner. The SE-edges and the N-corner remain very inconspicuous, whilst the forest-paths never appear. While Moore et al. (1970) - with regard to relevés - considered PCA-scatter diagrams in many respects more satisfactory than cluster analysis dendrograms, the conclusions of other authors agree more with ours. A PCA of all stands, carried out by Grigal & Goldstein (1971), provided no distinct groups whilst an ordination of quadrats gave little insight into the data, despite the use of i.a. a centered PCA (Adam et al., 1975).

Of the six regularly exhibited clusters in this forest, the two clustering methods account for five of them, of which four occurring in both methods. They seem the most powerful tool to distinguish well outlined vegetations.

Summary

Cover and height data about 122 taxa were obtained from 115 quadrats laid out in systematic way in a mixed forest in the tangent area of the Flemish and Brabantine Districts (Belgium). They were submitted to three classification and one ordination technique ; the situation was described by repeatedly comparing the four principal forest-layers (first and second tree, shrub and herb layer) with the latter two. Taking into account the four layers, better results are gained with NAA and PCA whilst the two clustering methods (HG and UPGC) yield clearer defined clusters with two layers only.

Using the 5 % and 1 % stopping rules in NAA, the results are somewhat better with the latter. The use of taxa to cluster (HG and UPGC) or to ordinate (PCA) was disappointing in the former two. In PCA, a variance-covariance matrix was giving more and better interpretable gradients when applying taxa, a matrix of correlation coefficients was more suitable with relevés.

In all, six readily definable vegetation-types and a much more diffused seventh one (a remnant) could be distinguished. Of the three classification techniques, HG and UPGC account for five, NAA for only three of them.

Important factors seem to be hydrography and stratification of the forest

Samenvatting

In een gemengd bos van ongeveer 19 ha in het grensgebied van het Vlaams en het Brabantse Distrikt (België) werden 115 opnamen verricht in evenzovele systematisch uitgelegde proefvlakken. Drie cluster- en één ordinatie techniek werden toegepast. Normale Associatieanalyse (NAA) en Principale Componenten Analyse (PCA) gaven betere resultaten wanneer beide boomlagen, struik- en kruidlaag als één geheel werden beschouwd, de overige twee Clusteranalyses (HG en UPGC) echter wanneer de laatste twee apart werden bekeken. In de NAA leverde de haltdrempel van 1 % wat duidelijker groepen als die van 5 %. Povere resultaten werden verkregen met het klassificeren der taxa (nl. 122) zowel met HG, UPGC als PCA. Met PCA kwamen gradiënten duidelijker tot uiting wanneer de variantie-kovariantie matrix steunde op taxa en deze van korrelatiekoefficienten op opnamen. HG en UPGC waren in staat vijf vegetatietypen te onderscheiden, NAA echter enkel drie; in totaal zes goed en één veel minder te omschrijven vegetatietype.

Résumé

Dans un bois mixte de quelque 19 ha, sous aménagement forestier, situé dans la région frontrière des districts phytogéographiques Picardie - Brabanton et Flandrien (Belgique), 115 relevés relevés étaient pris dans un même nombre de quadrats placés systématiquement. Trois méthodes de classification et une méthode d'ordination étaient appliquées. L'analyse normale des associations interspécifiques (NAA) et l'analyse en composantes principales (PCA) donnaient les meilleurs résultats en considérant globalement les deux strates arborescentes et les strates arbustive et herbacée, les deux autres méthodes de classification (HG et UPGC) par contre seulement quand les deux strates les plus basses étaient examinées. Appliquant le NAA la délimitation des groupes était un peu mieux sur le seuil de 1 % que sur celui de 5 %. En classifiant ou en ordonnant les espèces, tous les résultats obtenus par les HG, UPGC et PCA étaient difficiles à interpréter. Appliquant le PCA et s'appuyant sur des espèces, une détection claire d'une gradient se produisait plus facilement avec une matrice de variances-covariances, par contre sur des relevés avec une matrice de corrélations.

HG et UPGC étaient capables de déterminer cinq types de végétation, mais NAA pas plus que trois ; pour l'ensemble des quatre analyses, six types de végétation distincts et un beaucoup plus confus.

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Tab. 1. Relevé (a) and coordinate numbers (b).

(a)	(b)	(a)	(b)	(a)	(b)
1	15.03/1	39	13.02/2	77	11.05/3
2	14.02/4	40	12.02/4	78	12.04/2
3	14.03/3	41	13.03/1	79	12.05/1
4	13.04/3	42	11.04/3	80	11.04/4
5	14.03/2	43	12.03/2	81	11.04/1
6	14.04/1	44	12.04/1	82	10.04/3
7	13.03/4	45	08.05/3	83	10.04/2
8	13.04/2	46	08.04/2	84	09.05/3
9	12.04/4	47	08.05/2	85	10.05/1
10	12.05/3	48	03.05/1	86	09.04/4
11	13.05/1	49	08.04/4	87	08.03/4
12	11.04/2	50	07.06/3	88	09.04/1
13	10.05/3	51	08.06/1	89	08.03/1
14	10.04/4	52	07.05/4	90	09.03/2
15	11.05/1	53	06.04/4	91	09.03/3
16	10.04/1	54	07.04/2	92	09.05/2
17	09.03/4	55	06.05/3	93	08.06/3
18	09.04/3	56	07.05/1	94	08.06/2
19	10.03/2	57	13.05/3	95	08.05/4
20	09.02/2	58	14.04/2	96	09.06/1
21	08.03/3	59	14.05/1	97	09.06/4
22	09.03/1	60	13.04/4	98	11.05/2
23	08.02/4	61	14.05/4	99	10.05/4
24	10.05/2	62	14.06/3	100	11.06/1
25	09.06/3	63	15.06/1	101	11.06/3
26	09.05/4	64	15.05/2	102	11.05/4
27	08.07/3	65	14.04/3	103	07.05/3
28	09.06/2	66	15.03/2	104	08.04/2
29	08.06/4	67	15.04/1	105	07.05/2
30	09.07/1	68	14.03/4	106	07.04/1
31	15.04/2	69	14.03/1	107	07.04/4
32	14.05/3	70	13.02/4	108	12.04/3
33	14.04/4	71	13.03/3	109	08.05/1
34	15.05/1	72	14.02/2	110	08.04/3
35	12.05/4	73	13.03/2	111	08.03/2
36	14.06/2	74	13.04/1	112	07.04/3
37	14.05/2	75	12.03/4	113	08.02/1
38	12.03/3	76	12.03/1	114	07.03/4
				115	13.05/2

Table 2. Taxa found in the "Aalmoesensiebos" (Gontrode, 50°49' N., 3°48'E.) during August and September 1974, with their code- and variatenummer(s).

<i>Acer pseudoplatanus</i>	0002	2- 5	<i>Dryopteris dilatata</i>	0419	51
<i>Aegopodium podagraria</i>	0011	6	<i>Dryopteris carthusiana</i>	0426	52
<i>Agrostis gigantea</i>	0017	7	<i>Epilobium angustifolium</i>	0450	53
<i>Agrostis tenuis</i>	0019	8	<i>Equisetum arvense</i>	0462	54
<i>Ajuga reptans</i>	0024	9	<i>Erica tetralix</i>	0473	55
<i>Alnus glutinosa</i>	0036	10-11	<i>Eupatorium cannabinum</i>	0490	56
<i>Alnus incana</i>	0037	12-13	<i>Fagus sylvatica</i>	0513	57-60
<i>Angelica sylvestris</i>	0060	14	<i>Filipendula ulmaria</i>	0526	61
<i>Anthoxanthum odoratum</i>	0066	15	<i>Frangula alnus</i>	0530	62-64
<i>Anthriscus sylvestris</i>	0070	16	<i>Fraxinus excelsior</i>	0531	65-68
<i>Arctium minus</i>	0084	17	<i>Galeopsis tetrahit</i>	0543	69
<i>Arrhenaterum elatius</i>	0096	18	<i>Galium palustre</i>	0552	70
<i>Arum maculatum</i>	0103	18	<i>Geranium robertianum</i>	0576	71
<i>Athyrium filix-femina</i>	0119	20	<i>Geum urbanum</i>	0579	72
<i>Betula pubescens</i>	0139	21-24	<i>Glechoma hederacea</i>	0582	73
<i>Betula pendula</i>	0140	25-27	<i>Hedera helix</i>	0598	75-78
<i>Blechnum spicant</i>	0146	28	<i>Heracleum sphondylium</i>	0607	79
<i>Brachypodium sylvaticum</i>	0151	29	<i>Holcus lanatus</i>	0631	80
<i>Cardamine pratensis</i>	0205	30	<i>Holcus mollis</i>	0632	81
<i>Carex pilulifera</i>	0251	32	<i>Humulus lupulus</i>	0639	82
<i>Carex remota</i>	0258	33	<i>Ilex aquifolium</i>	0658	83
<i>Carex sylvatica</i>	0264	34	<i>Juncus subuliflorus</i>	0679	84
<i>Carpinus betulus</i>	0270	35	<i>Juncus effusus</i>	0680	85
<i>Castanea sativa</i>	0273	36-39	<i>Juncus tenuis</i>	0690	86
<i>Cirsium palustre</i>	0335	40	<i>Lamium album</i>	0700	87
<i>Cornus sanguinea</i>	0355	41	<i>Lamium galeobdolon</i>	0702	88
<i>Corylus avellana</i>	0366	42-44	<i>Lamium purpureum</i>	0706	89
<i>Crataegus monogyna</i>	0369	45	<i>Lonicera periclymenum</i>	0759	90-93
<i>Crataegus laevigata</i>	0370	46	<i>Luzula pilosa</i>	0770	94
<i>Dactylis glomerata</i>	0390	49	<i>Lycopus europaeus</i>	0780	95
<i>Deschampsia cespitosa</i>	0397	50	<i>Lysimachia nummularia</i>	0782	96

<i>Lysimachia vulgaris</i>	0784	97	<i>Rumex</i> o. ssp. <i>obtusifolius</i>	1101	139
<i>Maianthemum bifolium</i>	0786	98	<i>Rumex sanguineus</i>	1103	140
<i>Malus sylvestris</i>	0787	99	<i>Salix alba</i>	1116	141
<i>Melica uniflora</i>	0808	100	<i>Salix cinerea</i>	1118	142-143
<i>Mercurialis perennis</i>	0823	101	<i>Sambucus nigra</i>	1133	144-145
<i>Molinia caerulea</i>	0832	102	<i>Solidago virgaurea</i>	1222	147
<i>Myosoton aquaticum</i>	0847	103	<i>Sortus aucuparia</i>	1227	148-150
<i>Oxalis acetosella</i>	0909	104	<i>Stachys sylvatica</i>	1246	151
<i>Plantago major</i>	0947	105	<i>Stellaria holostea</i>	1249	152
<i>Poa annua</i>	0952	106	<i>Stellaria media</i>	1250	153
<i>Poa palustris</i>	0957	107	<i>Taxus beccata</i>	1267	155
<i>Poa trivialis</i>	0959	108	<i>Teucrium scorodonia</i>	1273	156
<i>Polygonatum multiflorum</i>	0984	109	<i>Tussilago farfara</i>	1316	157
<i>Polygonum hydropiper</i>	0972	110	<i>Urtica dioica</i>	1321	158
<i>Populus tremula</i>	0983	111	<i>Valeriana repens</i>	1333	159
<i>Potentilla erecta</i>	1008	112	<i>Viburnum opulus</i>	1367	160-161
<i>Potentilla sterilis</i>	1011	113	<i>Vinca minor</i>	1377	164
<i>Primula elatior</i>	1015	115	<i>Viola reichenbachiana</i>	1386	165
<i>Prunella vulgaris</i>	1017	116	<i>Rubus</i> sp.	1402	166-167
<i>Prunus avium</i>	1018	117-119	<i>Quercus rubra</i>	1406	168-171
<i>Prunus padus</i>	1019	120-121	<i>Larix kaempferi</i>	1407	172-174
<i>Prunus serotina</i>	1020	122-124	<i>Amelanchier lamarckii</i>	1408	175-176
<i>Prunus spinosa</i>	1021	125-126	<i>Robinia pseudacacia</i>	1411	177-178
<i>Pteridium aquilinum</i>	1022	127-128	<i>Ulmus glabra</i>	1451	179-181
<i>Quercus robur</i>	1037	129-132	<i>Euonymus europaeus</i>	2001	182
<i>Ranunculus flammula</i>	1048	133	<i>Populus x canadensis</i>	2002	183-186
<i>Ranunculus repens</i>	1056	134	<i>Pseudotsuga menziesii</i>	2003	-
<i>Ribes rubrum</i>	1071	135	<i>Abies grandis</i>		187
<i>Rosa canina</i>	1081	136-137	<i>Callitriche</i> sp.	2004	188
<i>Rubus idaeus</i>	1091	138	<i>Populus nigra</i>	2005	189

- Fig. 1. The "Aelmoeseneibos" forest (50°49'N, 3°48' E) near Ghent.
For further explanations : see text.
- Fig. 2. Cluster Analysis : dendrograms of vegetation-relevés, after Hierarchical Grouping (HG), using taxa occurring in (2a) four layers and (2b) the two lower layers. Dashed line : level on the maps 3a and 3b. First number-row : cluster-numbers, second number-row : number of vegetation-relevés.
- Fig. 3. Cluster Analysis : distribution of vegetation-relevés, after Hierarchical Grouping (HG), using taxa occurring in (3a) four layers and (3b) the two lower layers. Opposite to the recommendation of the dendrograms, clusters 1 and 2 (3a) and clusters 4, 5 and 6 (3b) are shown separately. Cluster symbols : \oplus = cluster 1, \ominus = cluster 2, \blacksquare = cluster 3, \otimes = cluster 4, \odot = cluster 5, \blacktriangle = cluster 6, \oplus = cluster 7. P = picnic site, M = abandoned meadows with young deciduous mixed plantations.
- Fig. 4. Cluster Analysis : distribution of structure-relevés, after Hierarchical Grouping (HG), using (4a) structural characters in the four layers and (4b) taxa in the two lower layers. Cluster symbols : see Fig. 3.
- Fig. 5. Cluster Analysis (unweighted pair-group centroid method : UPGC) of vegetation-relevés using taxa in (5a) four layers and (5b) the two lower layers. Cluster symbols : see Fig. 3.
- Fig. 6. Normal Association Analysis : distribution of vegetation-relevés using taxa occurring in four layers. Subdivision at a probability level of (6a) 5 % and (6b) 1 %. Cluster symbols : see Fig. 3.
- Fig. 7. Normal Association Analysis : dendrograms with subdivisions at a probability level of (7a) 5 % and (7b) 1 %. Used taxa occur in the two lower layers. For code-numbers : see Table 2. Dashed line : level on the maps 8a and 8b.
- Fig. 8. Like Fig. 6, but using taxa occurring in the two lower layers. Cluster symbols : see Fig. 3.
- Fig. 8c. Distribution of vegetation-relevés using structural characters from four layers. \odot = second tree layer and moss layer absent, \ominus = only second tree layer absent, \blacktriangle = only moss layer absent, \otimes = four layers present.
- Fig. 9. Principal Component Analysis of the variates or floristic variables occurring in the four layers : (9a) axes 1 and 2, (9b) axes 1 and 3. Variates laying between -0.02 and + 0.02 on both axes are not shown separately (n = 158 resp. 159).
- Fig. 10. Principal Component Analysis of (10a) a variance-covariance matrix between relevés (axes 1 and 2) using the taxa occurring in four layers, and (10b) a correlation matrix between the floristic variables (axes 1 and 3) occurring in the two lower layers. Variates in Fig. 10b laying between -0.1 and + 0.1 on both axes are not shown separately (n = 39).

Fig. 11. Principal Component Analysis of the relations between the vegetation relevés, using the floristic variables occurring in the two lower layers : (11a) a variance-covariance matrix, (11b) a correlation matrix. Axes 1 and 2. Variates in Fig. 11b laying between -0.5 and + 0.5 on both axes are not shown separately (n = 55).

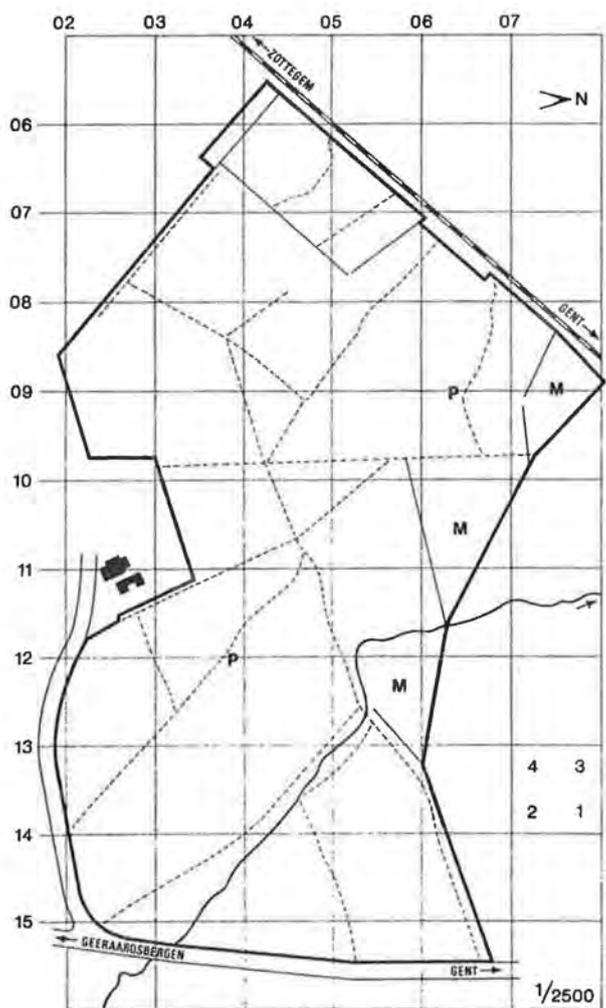


Fig. 1

Fig. 2a

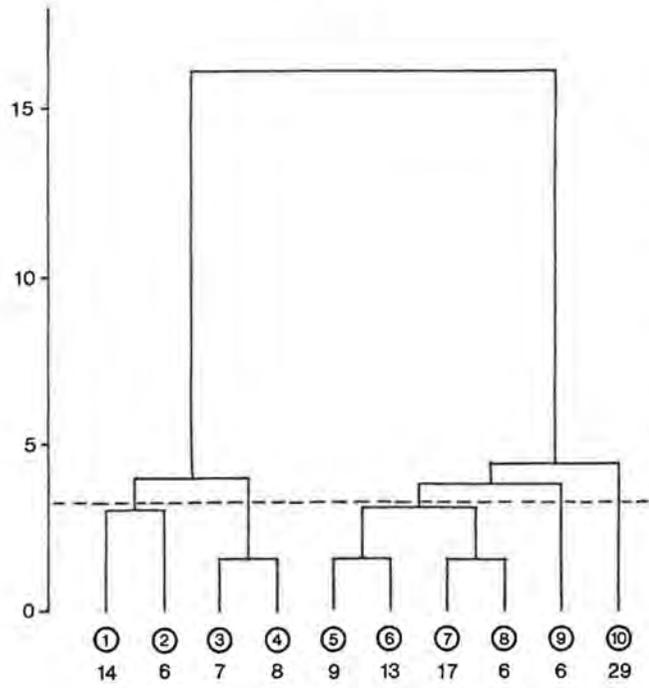
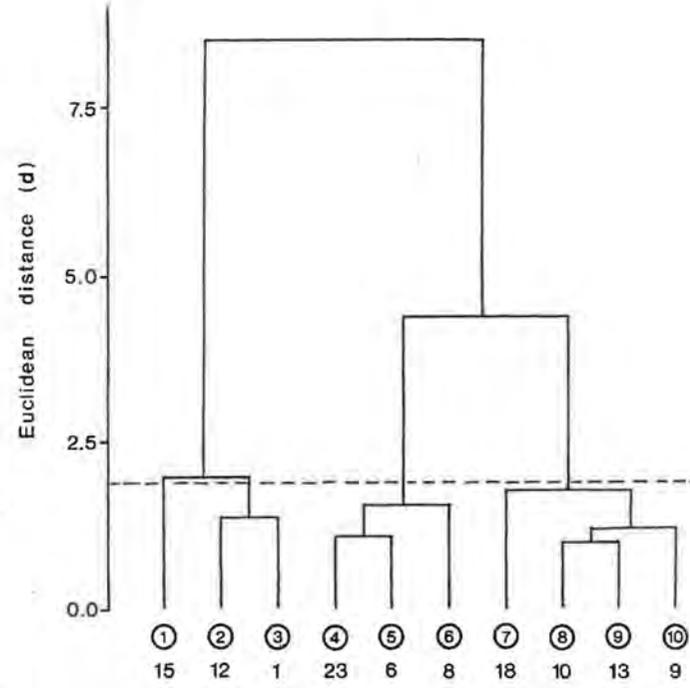
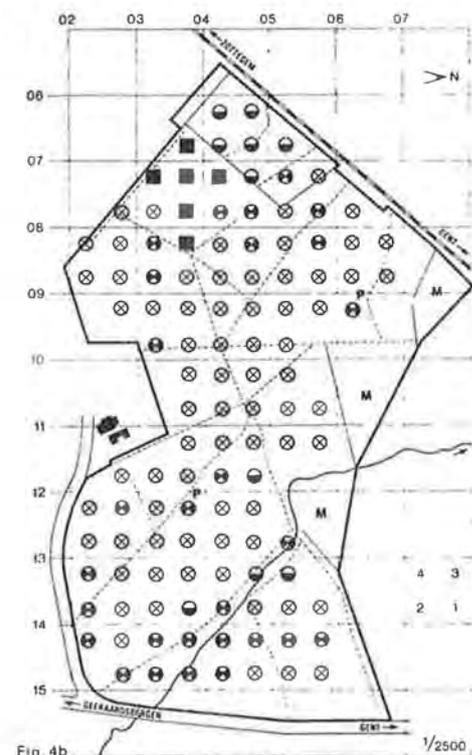
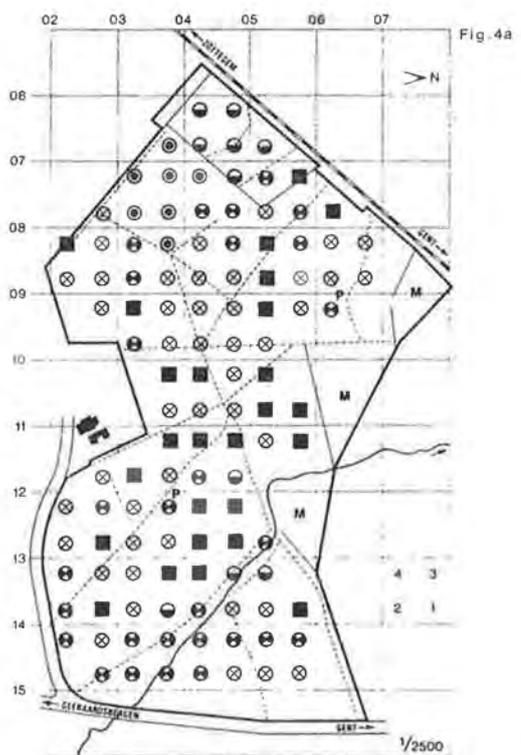
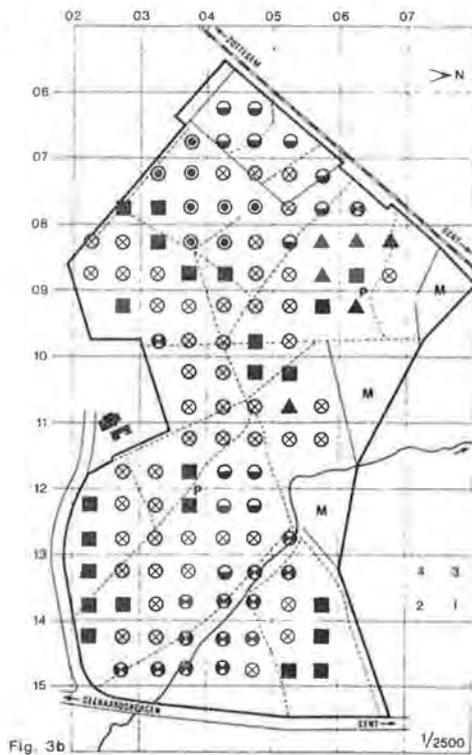
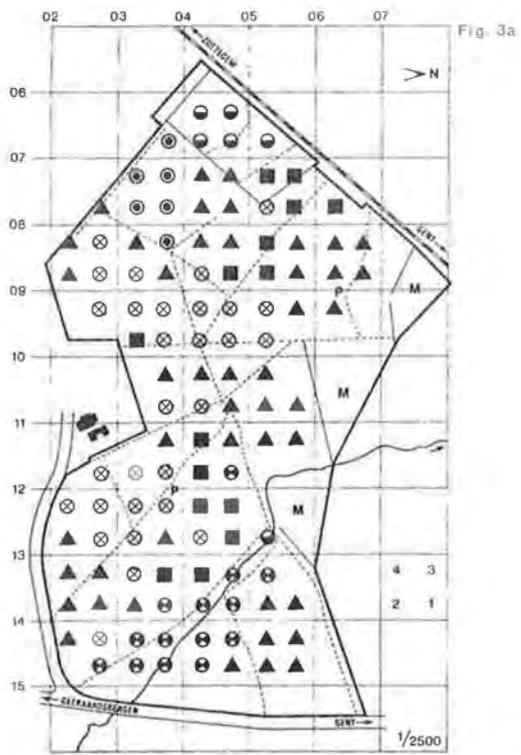
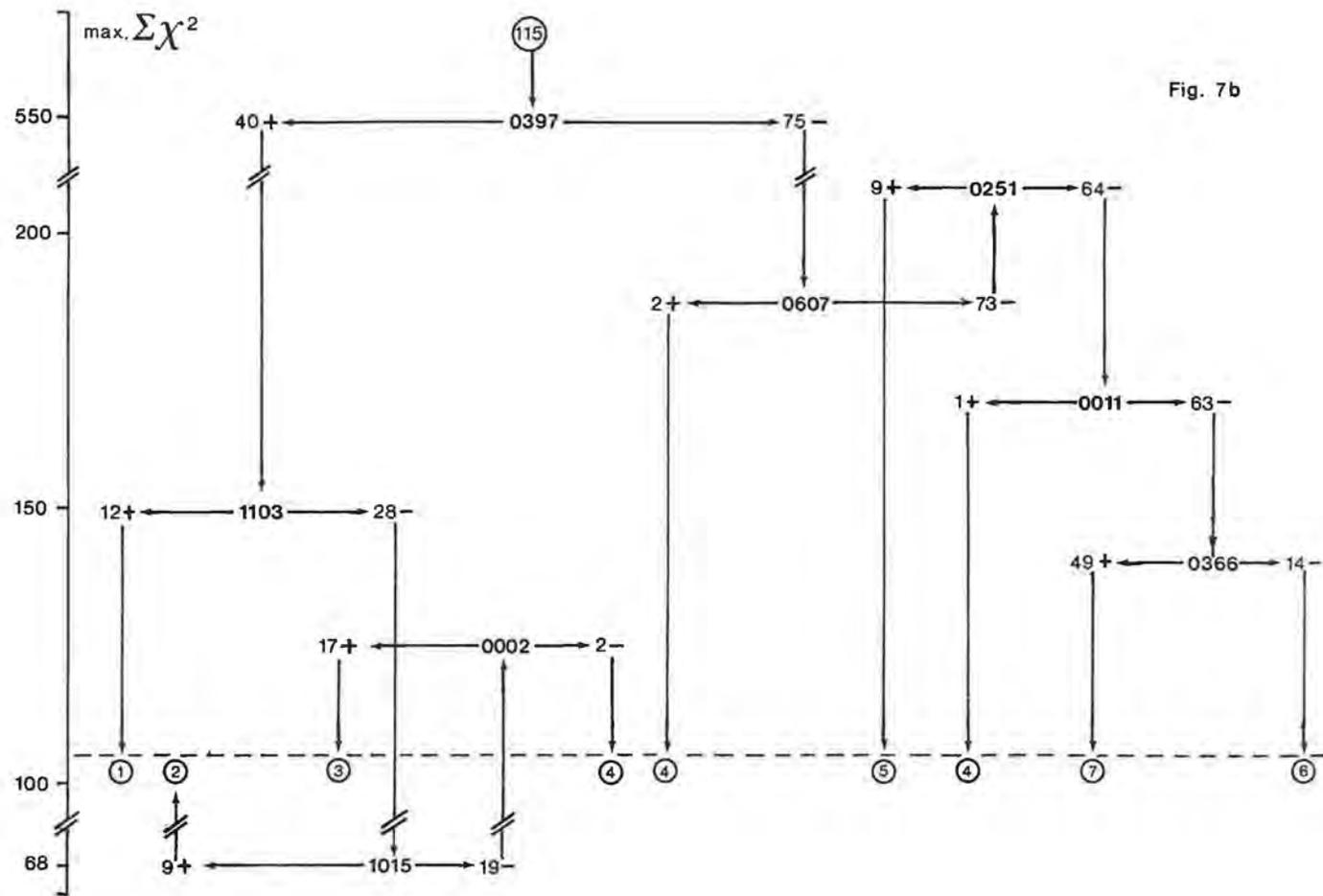


Fig. 2b







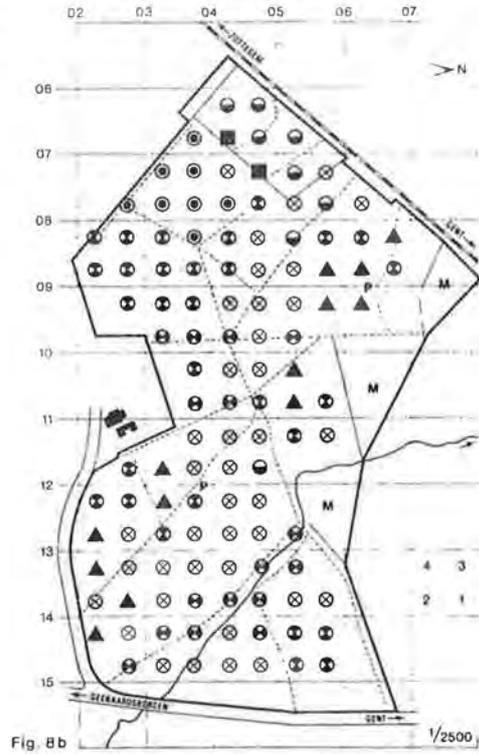
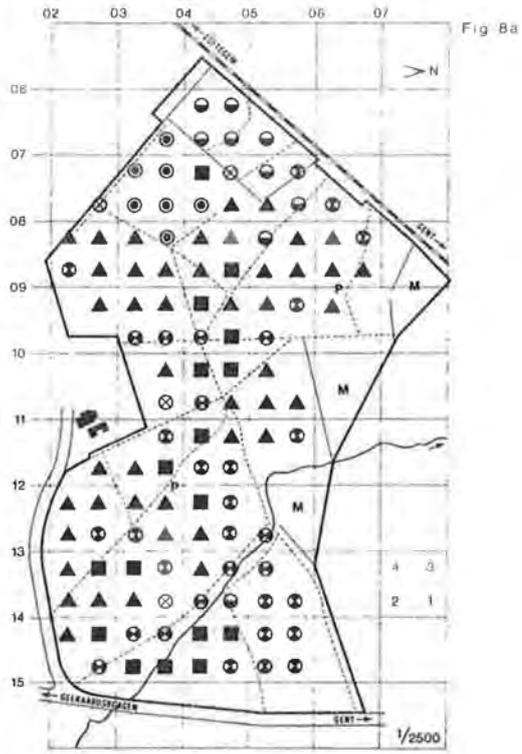


Fig. 8c

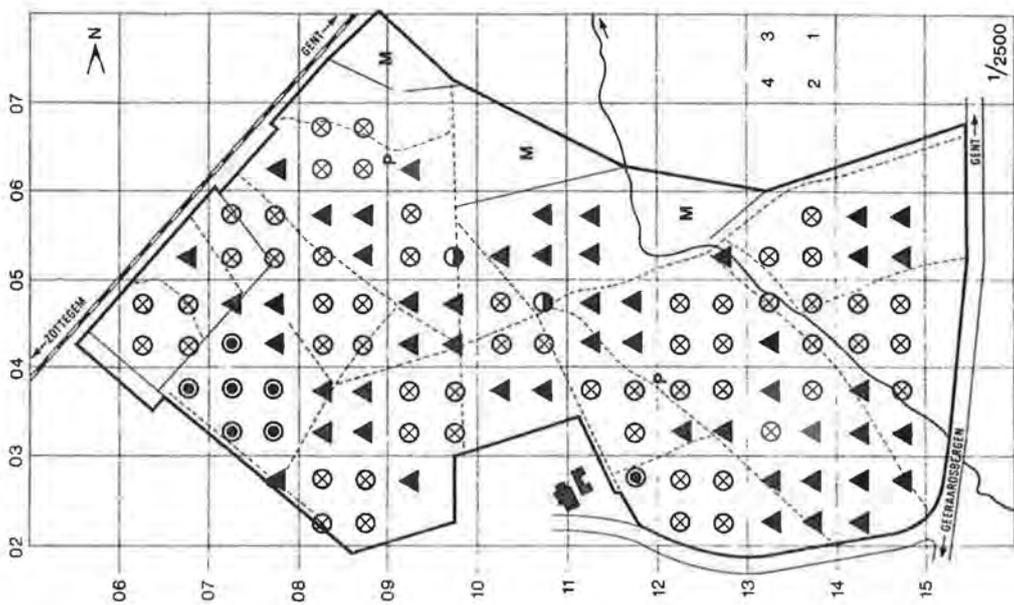


Fig. 9a

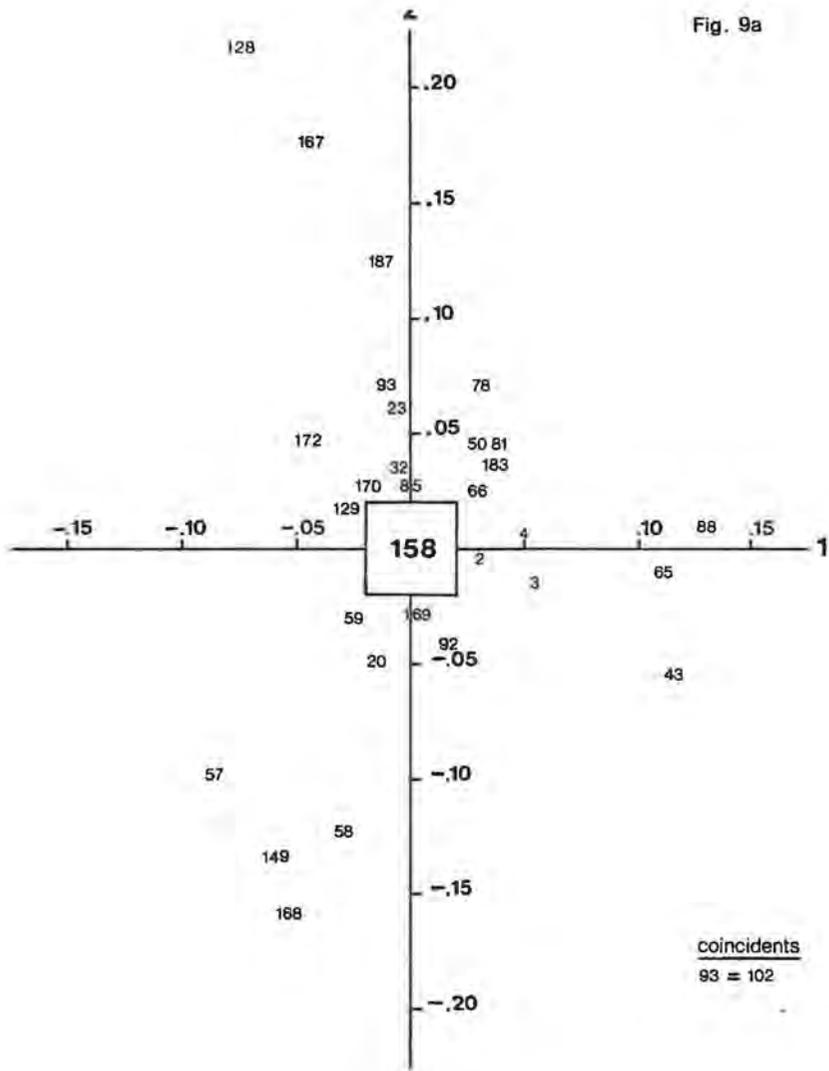


Fig. 9b

