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DETECTION OF SOME MICROPATTERNS OF WINTER ANNUALS IN PIONEER COMMUNITIES OF DRY SANDY SOILS

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SUMMARY

A new method for arranging vegetational data is described and applied to data from 20 cm square plots in pioneer communities of dry sandy soils in the north-western coastal dunes of the Dutch island Voorne. The presumed micropatterns within these communities are conveniently displayed by the relevé-groups distinguished by this method.

1. INTRODUCTION

This paper describes some preliminary studies concerning the problem of pattern and process in pioneer communities of dry sandy soils in the coastal dunes near Oostvoorne. This vegetation contains a relatively large number of winter annuals, such as *Aira praecox* L., *Arenaria serpyllifolia* L., *Cardamine hirsuta* L., *Cerastium semidecandrum* L., *Erophila verna* (L.) Chevallier, *Myosotis ramosissima* Rochel ex Schult., *Phleum arenarium* L., *Saxifraga tridactylites* L., *Silene conica* L., *Veronica arvensis* L., and *Vicia lathyroides* L.. These open communities can be found all over the investigated dune area, forming mosaics with dune grasslands and dune scrubs. Within these community pattern, "macropattern", the pioneer component occupies small areas, mostly only 10–50 sq.m. It shows a considerable variation in winter annual composition, partly described by VAN DER MAAREL & WESTHOFF (1964).

In synsystematical surveys, e.g. BOERBOOM (1960), WESTHOFF & DEN HELD (1969) and DOING (1966), however, this variation can not be recognized. Most of the winter annuals are considered as characteristic species either of the class Koelerio-Corynephoretea or of one of its associations, viz. the Tortulo-Phleetum. The unknown synsystematical and synecological significance of this variation formed the motive of the present research. During the first phase of this research it was found that within the pioneer communities an even more remarkable variation in the winter annual composition occurs. Very small homogeneous areas of only some sq.dm are occupied by distinct combinations of the annuals, each of them presumably reflecting a specific combination of habitat factors. It was then decided to concentrate research on this "micropattern".

Most recent studies concerning these winter annuals deal with their adaptation to extreme habitat conditions and with the developmental pattern of the annuals (HAJKOVA & KREKULÉ 1972; KREKULÉ & HAJKOVA 1972; NEWMAN

1963, 1967; RATCLIFFE 1961). In these studies the annuals are considered as members of the same ecological species group, having in common the ability to persist on open dry sandy soils. In the present study, however, the main object is the difference in the distribution patterns of these species in relation to the environmental variation.

In a study of this kind at least three consecutive phases can be distinguished (cf. CLAPHAM 1969; DALE 1970; ELLENBERG 1954):

a. analysis of vegetation data concerning these winter annuals, for an accurate detection of both macro- and micropatterns in the corresponding communities.
b. analysis of environmental data, for the establishment of correlations between the pattern in the distribution of either community types or single annuals with corresponding patterns in one or more environmental variables.
c. the establishment of causal relationships behind these correlations by means of "controlled" as well as "uncontrolled experiments" (FERRARI 1960). This paper is dealing with the first phase, particularly with a new computer method for structuring vegetational data.

2. METHODS

2.1. Sampling of vegetational data

The data were collected in 1971 in the north-western dunes of Voorne belonging to the "Stichting Het Zuid-Hollands Landschap" (Provincial Nature Protection Foundation of South-Holland). The vegetation of this area consists of mosaics of small and very different dominance communities as well as communities characterized by local species combinations. For a further description of this area see VAN DER MAAREL & WESTHOFF (1964). The sampling plots have a size of 20 cm square and have been selected so as to represent the variation in the contribution of the annuals to the total floristic composition of the different micropattern components. For the detection of this variation the size of 20 cm square appeared to be the most appropriate one. The percentage cover of all species in each quadrate was determined. The names of the species are according to HEUKELS & VAN OOSTSTROOM (1970).

2.2. Structuring of vegetational data

For the detection of pattern in the sampled material a normal phytosociological table was constructed, with the relevé data in the columns and the species data in the rows of the table. Then the table was structured on the basis of relevé and relevé-group similarities. Computations were carried out on the Nijmegen University's IBM 370/155 with a program written in FORTRAN IV. This program rearranges both the rows (species) and the columns (relevés) of the phytosociological table. This rearrangement consist of two consecutive parts:

a. an agglomerative classification of the relevés, in combination with a relocation procedure, leading to a set of relevé groups;
b. an ordering of relevés per relevé group, on the basis of between-group simi-

larities; an ordering of species on the basis of their presence in these groups.

2.2.1. The first part (relocation and fusion) operates in almost the same way as the program RELOC, one of the programs of the CLUSTAN IA packet of the computing centre of St. Andrews edited by WISHART (1969) and implemented at the IBM 370/155 at Nijmegen (FAST & JANSSEN 1970).

The procedure starts with an initial classification of the relevés which may be created by the investigator or at random by the computer. During a relocation scan the similarity between each relevé and the centroid of each cluster is computed on the basis of a (dis-)similarity coefficient selected by the user. When any relevé shows a greater similarity with a cluster other than its parent cluster, this relevé is moved to that cluster. The program repeats these relocation scans until all the clusters are stable, i.e. until no relevés are relocated during one full scan. Next, the similarities between all pairs of clusters are computed, the two clusters which are most similar are fused and the program returns to the relocation cycle to reset the relevés which appear to be misclassified at this stage of clustering. This procedure is continued either until the minimum number of clusters desired is obtained or until the similarity between the two most similar clusters drops below a minimum value to be specified by the user.

2.2.2. In the second part of the program (ordering of relevés and species in the table) the clusters as obtained in part one are consecutively placed in the table from the left to the right, either in order of their loadings on the first principal axis as computed by means of a successive Jacobi type solution (HORST 1965; HARMAN 1967) or in order of their resemblance to a selected "starting cluster". As "starting cluster" is selected either the cluster with the highest average similarity or the cluster with the highest value of the fraction: number of relevés belonging to that cluster/number of species "belonging" to that cluster, i.e. species whose frequency in that cluster exceeds a minimum frequency limit to be specified by the user. The relevés of this cluster are placed at the left of the table. Next, the relevés of the cluster which has most species in common with the preceding cluster are placed, etc. If none of the still unplaced clusters has any species in common with the last-placed cluster, a new starting cluster is selected from the remaining clusters and the procedure above described is continued until all relevés have been placed. The order of the relevés within the clusters is only determined by their initial rank number. Next, the species are placed in the table on the basis of their adherence to the clusters. First, species are placed belonging to the first but not to the second cluster; then species belonging to both clusters, next unplaced species belonging to the second cluster but not to the third, etc. The species not belonging to any cluster are placed at the bottom of the table in order of their initial rank number. With this program it is also possible to create clusters at two different hierarchic levels; it will be clear that while proceeding from the first to the second level only the fusion cycle and not the relocation cycle will operate. In this case the table is first ordered on the basis of the second set of clusters. Next, the relevés within those second level clusters comprising two or more clusters of the first level are rearranged per first level group according to the procedure described above. Species belonging neither to clusters of the first level nor to clusters of the second level are placed at the bottom of the table.

2.3. Indication of the differential value of species

Finally it is possible to indicate the irregularities of the distribution of species over the clusters by calculating with a chi-square test the probability that the difference between the observed frequency of a species in a certain cluster and the frequency expected on the basis of the frequency of that species in the whole set of relevés has been produced by chance alone. This computation may be useful in the determination of the differential value of a species in combination with the minimum frequency criterion mentioned above.

2.4. Ordination of the winter annuals

Starting with a correlation matrix based on Spearman's rank correlations between the winter annuals the loadings of the annuals on the first two principal axes are computed by means of a successive Jacobi type solution (HORST 1965; HARMAN 1967) in order to obtain a more direct scheme of relations between the winter annuals.

3. RESULTS

The relevé set structured by the program described above consists of 17 relevé groups at the 0.80 similarity level and 6 relevé groups at the 0.60 similarity level. The tabular ordering of the clusters at the 0.60 level is based on their loadings on the first pricipal axis which accounts for 65% of the total variance. The minimum frequency limit was specified at 60%. As similarity measure was selected the "similarity ratio" ($S = \Sigma x_i y_i / (\Sigma x_i + \Sigma y_i - \Sigma x_i y_i)$). Computing time for the structuring of this table was about one minute. A copy of this table is available on request.

In order to obtain a better insight into the hierachic relations between the relevé groups a dendrogram illustrating the fusion levels between the 0.80 and 0.60 stage is presented *(figure 1)*.

With the characterization of the different relevé groups four types of characteristic species can be distinguished for each group:

a. species with both a significant positive differential value and a frequency exceeding 60% in that relevé group;
b. species without a significant differential value but with a frequency exceeding 60% in that relevé group;
c. species with a significant negative differential value in that relevé group;
d. species with a significant positive differential value and a frequency smaller than 60% in that relevé group and a total frequency exceeding 5%.

The species characteristic for one or more relevé groups of the 0.60 level are presented in *table 1*.

Three clusters of the 0.80 level fusing at the 0.60 level (cf. *figure 1*) and show-

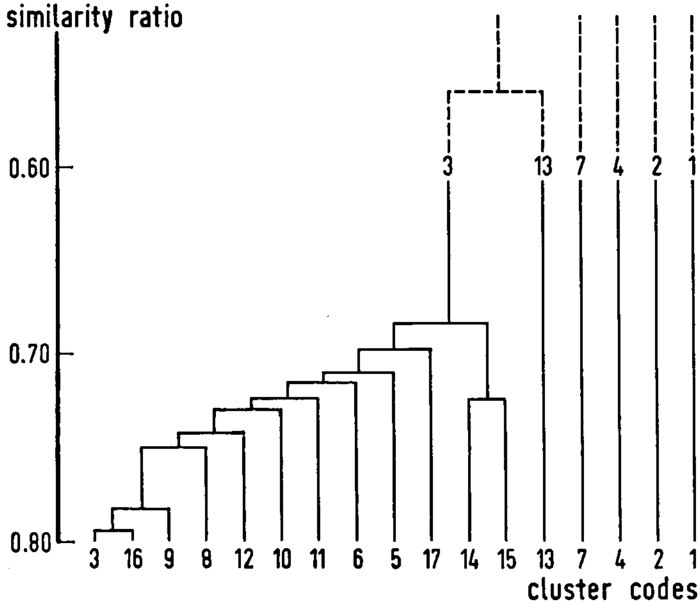

Fig. 1. Dendrogram presenting the hierarchical relations between the relevé groups at the 0.60 and 0.80 similarity level.

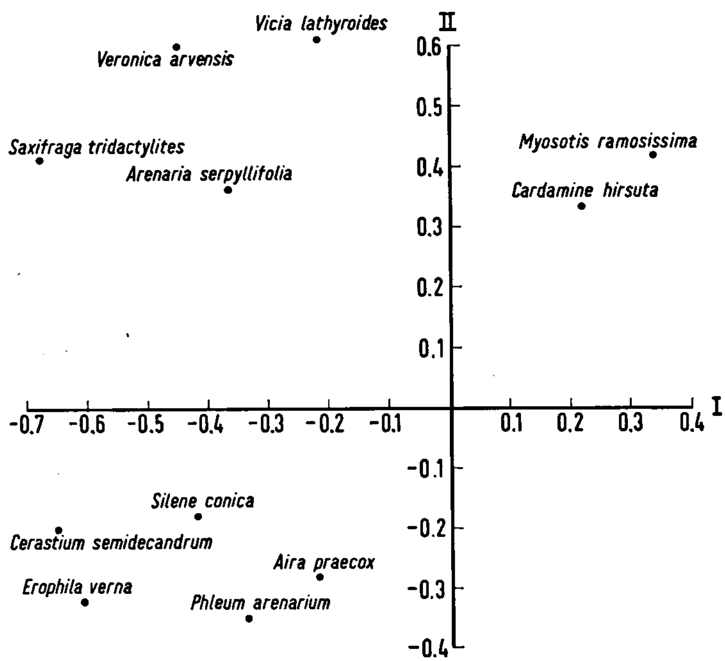

Fig. 2. Ordination of the winter annuals along the first two principal axes.

Table 1. Characterization of the clusters at the 0.60 similarity level. The symbols used correspond to the four types of characteristic species: a. positive differential and frequent (d); b. frequent but not differential (+); c. negative differential (—); d. positive differential but not frequent (!).
Notes: 1) *Hypnum cupressiforme* and/or *Brachythecium albicans*; 2) *Cladonia furcata* and/or *Cladonia rangiformis*

cluster code cluster size	7 4	1 7	13 13	2 3	4 5	3 144	total frequency
Phleum arenarium	+	—	—		—		0.52
Myosotis ramosissima		d	—		d		0.37
Poa pratensis		d		d			0.17
Cardamine hirsuta		d	d	d		—	0.14
Arenaria serpyllifolia			d				0.24
Erodium spec.			d				0.17
Cerastium semidecandrum	—	—	+	+	+	+	0.81
Veronica arvensis	—	—	+	+	—	+	0.58
Saxifraga tridactylites		—		+			0.42
Erophila verna			—	+			0.43
Aira praecox				d			0.18
Taraxacum spec.				d			0.13
Poa annua	!		!	d			0.06
Sedum acre		—	—	+	+	+	0.61
Festuca rubra				d	d		0.36
Tortula ruraliformis		—	—		+		0.38
Hypnum cupressiforme[1]	—	—		—	—	d	0.72
Bromus mollis			!				0.27
Cladonia furcata[2]						!	0.35
Galium verum			!				0.27
Carex arenaria						!	0.33
Hypochaeris radicata			!				0.15
Crepis capillaris			!				0.09
Trifolium dubium			!				0.07

Table 2. Characterization of some clusters at the 0.80 similarity level. The species groups correspond to the different types of characteristic species (cf. *table 1*). Notes see *table 1*.

I. cluster 14 (size = 10)	II cluster 16 (size = 30)	III. cluster 3 (size = 15)
a. *Bromus mollis*	a. *Phleum arenarium*	a. *Myosotis ramosissima*
Rumex acetosella	*Veronica arvensis*	*Tortula ruraliformis*
Cladonia furcata[2]	*Saxifraga tridactylites*	*Hypnum cupressiforme*[1]
Vicia lathyroides	*Erophila verna*	
Galium verum	*Tortula ruraliformis*	
Cerastium arvense	*Hypnum cupressiforme*[1]	
Plantago lanceolata		
b. *Cerastium semidecandrum*	b. *Cerastium semidecandrum*	b. *Cerastium semidecandrum*
Sedum acre	*Sedum acre*	*Sedum acre*
Veronica arvensis		
Saxifraga tridactylites		
Hypnum cupressiforme[1]		
c. *Phleum arenarium*		c. *Arenaria serpyllifolia*
Tortula ruraliformis		*Cladonia furcata*[2]
		Vicia lathyroides

ing the greatest distance on the first two principal axes, viz. cluster 3, 14, and 16, are characterized by a direct listing of the characteristic species per cluster *(table 2)*.

The position of the 11 winter annuals along the first two principal axes, together accounting for only 35% of the total variance, is presented in *figure 2*. This figure may be compared with *table 3* which presents the position of the winter annuals in the 17 clusters at the 0.80 level.

4. DISCUSSION

Most of the clusters contain elements of one or more associations of the alliance Galio-Koelerion (WESTHOFF & DEN HELD 1969), especially of the associations Tortulo-Phleetum and Taraxaco-Galietum. It is not possible to classify all relevé groups into lower rank units of the Braun-Blanquet system (BOERBOOM 1957, 1960; DOING 1964, 1966; WESTHOFF & DEN HELD 1969). This can be explained by the fact that the size of the sample plots in this study is small compared with the sample size usually selected in phytosociological studies of such vegetation types; further the selection of the plots has not been based on the total floristic assemblage. This procedure can result either in relevés transitional between two or more synsystematical units or in relevés containing a number of species too small to assign them to one of these units. However, it will be clear that cluster 3 at the 0.60 level belongs to the alliance Galio-Koelerion and that within this cluster at the 0.80 level groups belonging to the Erodio-Koelerion albescentis (i.e. cluster 3 and 16) and the Luzulo-Koelerion albescentis (i.e. cluster 14) can be distinguished. It appears from *table 3* and *figure 2* that the classification at the 0.80 similarity level is appropriate for the detection of winter annual combinations. The clusters at the 0.60 level, at least cluster 3, are too heterogeneous to show a clear distribution pattern of these species. Many different local combinations of winter annuals, each of them presumably reflecting a

Table 3. Position of the winter annuals in the clusters at the 0.80 similarity level (frequency exceeding 60%).

cluster code	7	1	13	2	4	16	5	11	12	9	10	6	3	15	14	17	8
cluster size	4	7	13	3	5	30	7	15	12	10	7	7	15	14	10	5	12
Phleum arenarium	+					+			+	+	+					+	+
Myosotis ramosissima		+			+					+			+				
Cardamine hirsuta		+	+	+													
Arenaria serpyllifolia			+						+	+						+	
Cerastium semidecandrum			+	+	+	+	+	+	+	+	+	+	+		+	+	+
Veronica arvensis			+	+		+		+	+		+			+	+		
Saxifraga tridactylites				+		+			+						+	+	
Erophila verna				+		+	+		+			+				+	+
Aira praecox				+				+									
Silene conica									+								
Vicia lathyroides														+	+	+	

definite combination of habitat factors, can easily be distinguished. The fact that the first two principal axes computed from the rank correlations between the winter annuals accounts for only 35% of the total variance, confirms the existence of this great variation. The next phase in this study will therefore be the establishment of correlations between the distribution of some annuals and some environmental variables.

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