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STUDIES ON THE VEGETATION DYNAMICS OF NANOCYPERION COMMUNITIES II. CLASSIFICATION AND ORDINATION OF SPECIES

I. BAGI and L. KÖRMÖCZI

Attila József University, Department of Botany, Szeged, Hungary

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Abstract

On the basis of the reciprocal averaging ordination studies on the species of the Nanocyperion-like cenoses, similarly to the ordination of the stands, the population of the Nanocyperion zone at the river-bed can be separated in two manners: interior primary succession characteristic to the lower relieves and exterior primary succession characteristic to the higher relieves. The development of the mean characteristic indicator values can be evaluated as the regular concomitant of these processes. The results of the ordination and the applied cluster analysis are well comparable. The development of the clusters shows connection with the distribution of the cenoses in time and space, i.e. with the vegetation dynamics of the river-bed' s mud vegetation.

Introduction

The rapid changes of the river-bed Nanocyperion associations make possible vegetation dynamic studies devoid of exterior effects and feasible under natural conditions, similarly to the qualitative description of the alterations of the flood-plain Bidentetea cenoses (BAGI and BODROGKÖZY 1984). In the first half of the studies the main determinations in respect to the regularities of the alterations of the Nanocyperion-like cenoses were as follows (BAGI 1985). It could be determined on the basis of the reciprocal averaging (RA) ordination studies on the stands that the relative repression of the hygrofrequent species is generally characteristic to the transformation of the vegetation at the studied area, the cause of which is the continuous drying out of the biotope. The relief-dependent appearance of the nitrofrequent species is characteristic. On the basis of the development of the partial coverage of the nitrofrequent species, two types of successions originating from the river-bed Nanocyperion stands could be distinguished. At higher relieves where the vegetation period is longer due to the earlier cessation of water covering, and the Nanocyperion associations are in direct contact with the Bidentetea (Chenopodio-Scleranthea) communities (TÍMÁR 1950a, b), the appearance of the nitrofrequent species is intensive in the second half of the vegetation period. This process leads to the early disintegration of the Nanocyperion associations, and Bidentetea communities develop. This type of succession can be regarded as exterior primary succession. The succession is exterior despite the fact that the major part of the propagules of the developing new community is found at the area even in the initial state, since the propagules originate from the zone of the higher relief which is by now not of Nanocyperion character, their replacement is already started during the Nanocyperion state of development. The syngenetic character is dominant in this succession process (PRÉCSÉNYI 1981).

At deeper relieves the appearance of the nitrofrequent species is not considerable, during the course of transformation the typically Nanocyperion elements are dispalced by species standing close to both the Bidentetea association-class and the Nanocyperion association-group *(Potentilla supina, Rumex stenophyllus)*, the less hygrofrequent Nanocyperion *(Gnaphalium uliginosum)* and non-nitrofrequent Chenopodio-Scleranthea *(Rorippa sylvestris, Lythrum salicaria)* (Soó 1964—80). This type of succession can be regarded as interior primary succession, because the penetration of the foreign elements at the area is minimal and the dominance values of the hygrofrequent species of the highly hygrophytic Nanocyperion stands decrease to the benefit of the less hygrofrequent species as the consequence of accomodation to dryness. The interior primary succession can also be regarded as change of aspect, in the traditional sense. In the case of the Nanocyperion associations, however, the Nanocyperion — Chenopodio-Scleranthea transformation is so expressed that it oversteps the concept of change of aspect, therefore it can be mentioned as primary succession. The ecogenetic character dominates in the process manifested in accomodation to dryness by a change in species composition.

The studies on classification and ordination in the first part were related to the cenoses and relevés. The described results were gained on the basis of the interpretation of these methods. The question arises whether, subjecting the species to the already applied methods, the afore-mentioned regularities could be evidenced; whether the multivariate analysis of the species would result newer relationships?

The various types of „multivariate analyses" (ORLÓCZI 1975, SZŐCS 1972) are widely used in ecological practice. The most widely used are the classification and ordination methods. Several publications have reported on the possibilities (SVÁB 1979), conditions (SZŐCS 1973), weakness (HILL-GAUCH 1980) and defects (BEALS 1973) of application of the various methods. Reports on the testing of the various methods are also numerous (SWAN 1970, NOY-MEIR-AUSTIN 1970, GAUCH 1982a). The joint application of the methods is frequent; comparative studies on the methods, e.g. application of ordination methods besides regressionanalysis, D^2-analysis (PRÉCSÉNYI 1969), cluster analysis (GAUCH-WHITTAKER 1981).

The multivariate analysis may aim at studies on the species as well as the samples and stands. The multivariate analysis of species is generally used to solve taxonomic (HORÁNSZKY 1960) and cenosystematic (MUCINA 1982) problems. Furthermore, the species analysis is often used to clarify the correlations between environmental parameters and the structure of cenoses (GOLDSMIDT 1973). The ordination studies of species may confirm the results of other statistical methods, like interspecific associations (BATES 1975), non-metric multidimensional scaling (MATTHEWS 1978).

Materials and methods

The base of the calculations was the cenological table published in the first part of this report (Table 1).

The cenosystematic characterization of the species was performed on the basis of the summarizing work by Soó, with particular regard to the cenological references found in Volume VI. (Soó 1964—80).

The classification was performed by applying three different kinds of uniting methods strating from a similarity matrix calculated on the basis of the Rekonen-index: single linkage, complete linkage, simple average (PODANI 1980). The RENKONEN-index is:

$$S_{jk} = \sum_{i} \min\{p_{ij}, p_{ik}\}$$

Table 1

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
1. *Cyperus fuscus*	20	2	17	10	20	4	11	+	17	+	58	+
2. *Dichostylis micheliana*	36	2	43	6	38	+	11	+	9	+	2	+
3. *Gnaphalium uliginosum*	8	5	5	17	6	9	8	+	3	+	1	5
4. *Veronica anagallis-aquatica*	2	3	1	+	+		3	2				
5. *Rumex stenophyllus*	4	21	2	7	2	17	1	4		4		2
6. *Potentilla supina*		5		2		4		1		2		
7. *Plantago major*	8	9	9	3	10	9	4	6	9	10	17	4
8. *Rorippa sylvestris*	4	9	4	22	5	34	8	3	9	10	6	1
9. *Amaranthus lividus*	+	4	+	1	2	7	2	+	3	+	2	3
10. *Chenopodium rubrum*	5	2	2	17	3	4	12	4	5	7	+	2
11. *Lythrum salicaria*	7	17	7	4	4	3	8	8	7	10	+	8
12. *Xanthium italicum*		2	3	+			8	6	1	1	3	10
13. *Bidens tripartita*		1		1	+	2	1	6	+	1	+	15
14. *Agrostis stolonifera*		+		4		1		+	+	6	+	10
15. *Polygonum lapathifolium*	2	+	1	+	3	+	15	26	3	4	+	3
16. *Polygonum hydropiper*								8	+	6		
17. *Chenopodium album*		1		+			+	4	4	8		2
18. *Echinochloa crus-galli*	2	3	2	2	3	3	1	14	13	13	6	20
19. *Lythrum virgatum*		+	1	+		+	3	2	4	3		
20. *Tanacetum vulgare*		4		1	1	3	1	5	+	4		+
21. *Chenopodium polyspermum*			+		2		2		3			+
22. *Salix triandra (juv)*		1	1				+	+	4	4	3	+
23. *Portulaca oleracea*					1	+			3	2		

where, applied in the given case
I_{jk} is the similarity of species.—j and k-according to their covering values
p_{ij}, p_{ij} are the probabilities of finding of the species j and k, in the ith stand.

The reciprocal averaging technique was applied in the ordination calculations according to the method described by Hill, with the difference that the set of starting scores for the species consisted of random numbers between 0—100 (Hill 1973). The cause of the method selection was partly the objectivity of the RA opposed to the polar ordination (Gauch—Whittaker—Wentworth 1977) or the weighted averages ordination, and partly the „meaningful" ordination of species of the RA. The RA ordination is especially suitable for the processing of a base matrix (cenological table) composed of moderately heterogeneous data. For the ordination of an extremely heterogeneous mass of data, the detrended correspondence analysis (DCA) (Hill—Gauch 1980) developed for eliminating the errors of RA is more suitable, while the ordination of homogeneous data can be accomplished the most effecticely with the PCA ordination (Gauch 1982b). The less effective ordination of species of the PCA method is probably due to the fact that the data of the cenological tables can be regarded as more heterogeneous in respect to species, than to stands. Owing to the less informative character of the ordination of species in the case of PCA, authors usually apply the PCA ordination of stands to demonstrate the effect of species-related, mostly environmental parameters, comparing the various species' distribution among the objects (Ward 1970, Rogers 1970). Some authors use other methods for the ordination of species, apart from the PCA ordination of stands (zhang 1983).

Faults of RA are that the axes of higher serial number are determined by the lower ones, they are poor in surplus information and the median-related crowing of the objects are demonstrable at the end values of the 1. axis (Gauch 1982b). The degree of axes' independence from other can be checked by calculating the determination coefficient calculated on the basis of the linear regression (Sváb 1981). Naturally, the standard errors of the method cannot be excluded in such manner, since these do not change according to linear function. The determination coefficient expressing the subor-

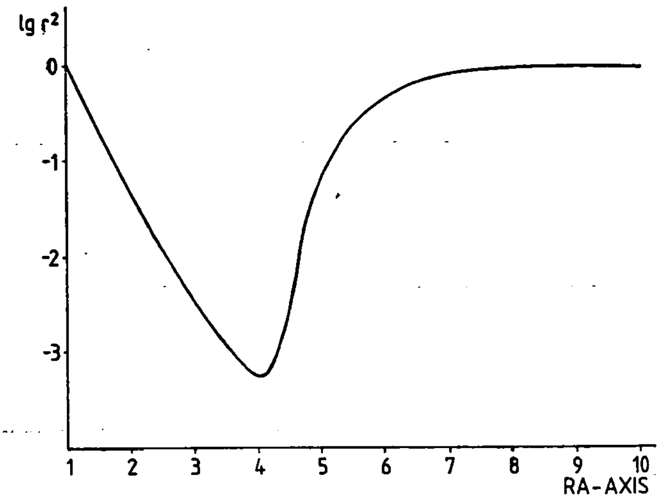

Fig. 1. Change of the determination constant (r^2) in the function of the increase in axis number (on the basis of the data shown on Table 1). The relationship of two variables is expressed by the determination coefficient. In the case of the 1—4 axes regarding the axes as variables the determination coefficient has a minimum, the regression between the two axes is minimal

dination between the first and higher axes develops as follows, in the function of the serial number of the axes (Fig. 1):

The determination coefficient is the lowest between the first and 4th axis (cp. GAUCH 1980). However, comparing the ordination figure with the result of the cluster analysis, the clusters of the dendrogram are the best differentiated between the 1—3 axis pairs, in this case the error arising from the regression of the axes as well as the standard error of the ordination are presumably of opposed gisns.

Results

Classification

With the application of the complete linkage and group average uniting types clusters made up of the same elements can be distinguished (PODANI 1980). The main groups are the followings:

The first group comprises the Nanocyperion character species *(Cyperus fuscus, Dichostylis micheliana, Gnaphalium uliginosum)* and the *Plantago major* ssp. *pleiosperma,* the character species of the Isoëto-Nanojuncetea class (PIETSCH 1973). Those species also assemble in this group, which are present at the area with a significant coverage even at the time of the initial stage of the Nanocyperion associations *(Lythrum salicaria, Chenopodium rubrum)*. As the character species of the Chenopodion fluviatile group *Chenopodium rubrum* proves the cenosystematic relationship between the Nanocyperion and the Chenopodion fluviatile association groups.

Such elements belong to the second group, which show the late stage of the vegetation at the river-bed Nanocyperion zone. On the basis of their occurrence, the seare mainly transitional elements: Nanocyperion — Bidentetea *(Rumex stenophyllus, Potentilla supina, Veronica anagallis-aquatica)*, Nanocyperion — Chenopodio-Scleranthea *(Rorippa sylvestris)*.

The third group comprises those elements which can be found at the area with small coverages, cenosystematically these differentiate from the Bidentetea and Nanocyperion species dominating at the area. (It should be noted that although the Bidentetea association-class is a part of the Chenopodio-Scleranthea division, it can well be separated from the other classes of the division, thus the differentiation does not meet with any difficulties).

Besides the typically Bidentetea elements *(Bidens tripartita, Xanthium italicum)* the fourth group contains the *Agrostis stolonifera* and the *Echinocloa crus-galli.* These species occur at higher relieves with essentially higher covering than at the lower parts, their coverages become considerable at the end of the vegetation period.

The *Polygonum* species, the character species of the Bidention association group, are segregated in the fifth cluster, as is also the *Chenopodium album,* which has wide ability of accommodation and is cenologically indifferent. This species is mentioned in literature as the character species of the Chenopodio-Scleranthea division (Soó 1964—80).

With the application of simple average, the 2., 3. and 4. groups can be united at a common similarity level, the common characteristic of the 2. and 4. groups is their appearance in the later phases of the vegetation period. The united group is linked with the first group at a similarity level of 0.26. In the case of complete linkage the segregation of the 1., 3. and 2., 4., 5. groups is maximal. The common characteristic of the 1. and 3. clusters — distinguishing them from the 2., 4., 5. groups is that their covering quota is more significant in the early stage of the vegetation period, than in the late stage (Fig. 2a, 2b).

Table 2 demonstrates the relationships between the relieves and the phases of the vegetation period, with the changes of the covering values for the species forming the various clusters (Table 2). The table also shows the proportional distribution

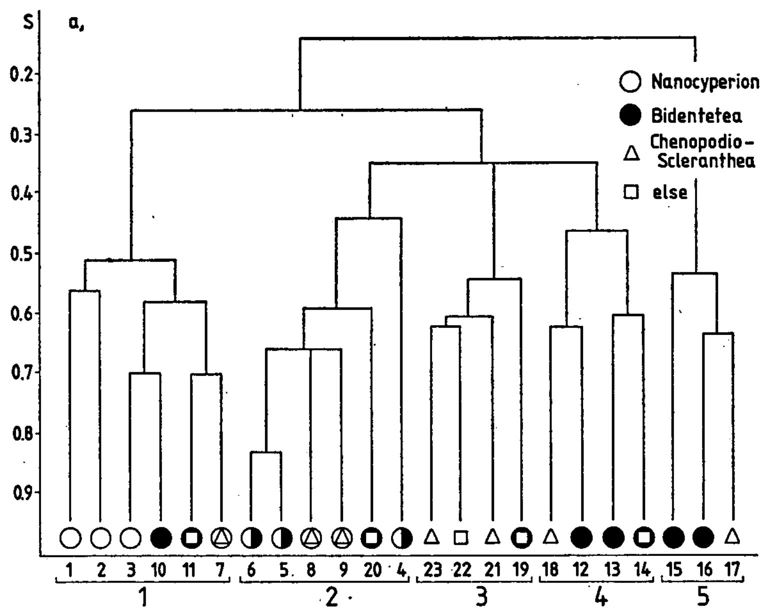

Fig. 2. a

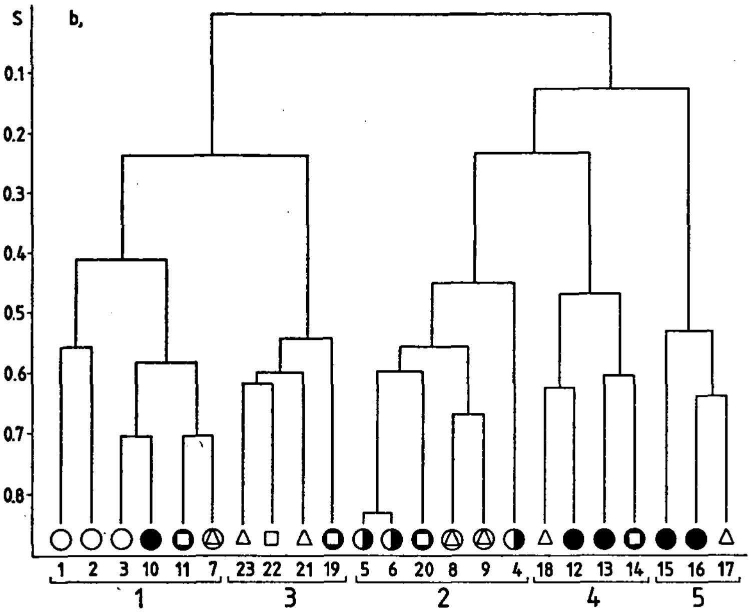

Fig. 2. b

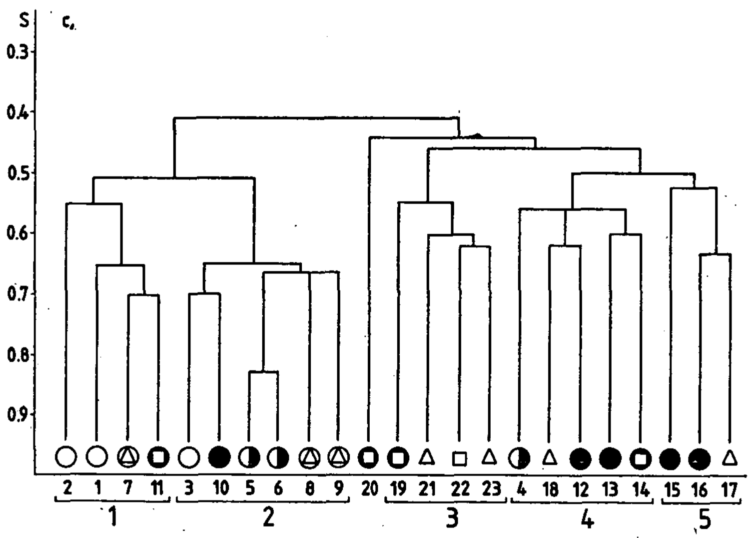

Fig. 2. c

Fig. 2. Dendrograms of cluster analyses prepared with a, simple averages, b, complete lincage and c, single linkage uniting techniques on the basis of the similarity matrix calculated with the Renkonen-index. The plant species can be identified on the basis of the serial number given in Table 1. The symbols drawn to the species refer to the cenological group(s) (combined symbols) where the occurrence of the given species is the most characteristic

among the various clusters of the vegetation covering at the area according to relief and time. It could be determined that progressing from the first towards the fifth cluster, the probability that the selected element of the cluster originates from a lower relief and an early time continuously decreases. The probability continuously increases that the element originates from a higher relief and besides this, is taken up at a later time. From the applied methods, this is emphasized principally by the single linkage method (although with slightly changed clusters) (Fig. 2c). In this case

Table 2

Cluster	A	B	C	D	p_A	p_B	p_C	p_D	p_{AC}	p_{AD}	p_{BC}	p_{BD}
1	64.75	42.48	72.88	34.12	0.6038	0.3962	0.6812	0.3188	0.4113	0.1925	0.2699	0.1263
2	27.92	13.45	10.00	31.20	0.6749	0.3251	0.2427	0.7573	0.1638	0.5111	0.0789	0.2462
3	1.05	5.84	4.58	2.19	0.1524	0.8476	0.6765	0.3235	0.1031	0.0493	0.5734	0.2742
4	5.06	23.54	7.29	21.72	0.1769	0.8231	0.2513	0.7487	0.0445	0.1324	0.2068	0.6163
5	1.22	14.69	5.25	10.77	0.0767	0.9233	0.3277	0.6723	0.0251	0.0516	0.3026	0.6207

A—lower relief
B—higher relief
C—early time
D—later time
$p_{A,B,C,D}$,—the probability of selection from the relevant cluster of element possering from the characteristic indicated in the index
$p_{AC,BD}$, —the probability of selection in respect to the element possessing both characteristics indicated in the index

the linkage effect only prevails at higher uniting levels, the major groups are essentially unchanged. Two elements of the first cluster *(Chenopodium rubrum* and *Gnaphalium uliginosum)* can be combined with the remaining elements of the second cluster. Those elements which join the second cluster — also doing so at a lower similarity level during the course of the previous uniting procedures — *(Tanacetum vulgare, Veronica angallis-aquatica)* segregate from the second, and even the first group, too. The first and second clusters combine at a similarity level of 0.51. The species of the combined clusters appear with greater covering at the lower relief of the study area. The segregation of the clusters bearing the serial numbers 3., 4., 5. in the previous combination is similar to the preceding ones in the case of single linkage combination.

Ordination

The results of the RA ordination of the species are observable on Fig. 3a. b. c. d. The species characteristic to cenosystematically identical categories can be segregated well. The objects can approximately be arranged into two groups „branches" (Fig. 3a). One branch is mainly formed by Nanocyperion elements, the other mainly by Bidentetea elements. The „transitional" species can be found at the crossing as well as at the common section of the branches. *(Veronica anagalis-aquatica* and *Rumex stenophyllus, Potentilla supina,).* The third group also segregated by the cluster

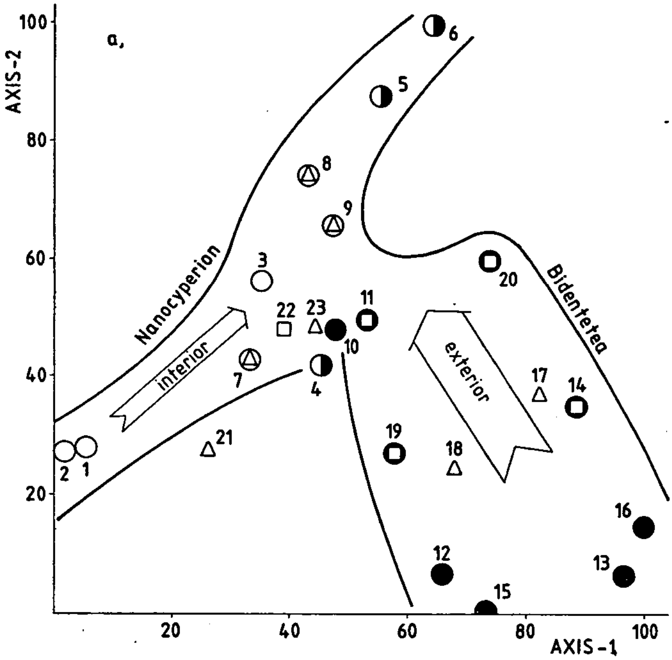
a,
AXIS-2
AXIS-1
Nanocyperion
interior
exterior
Bidentetea

Fig. 3.a

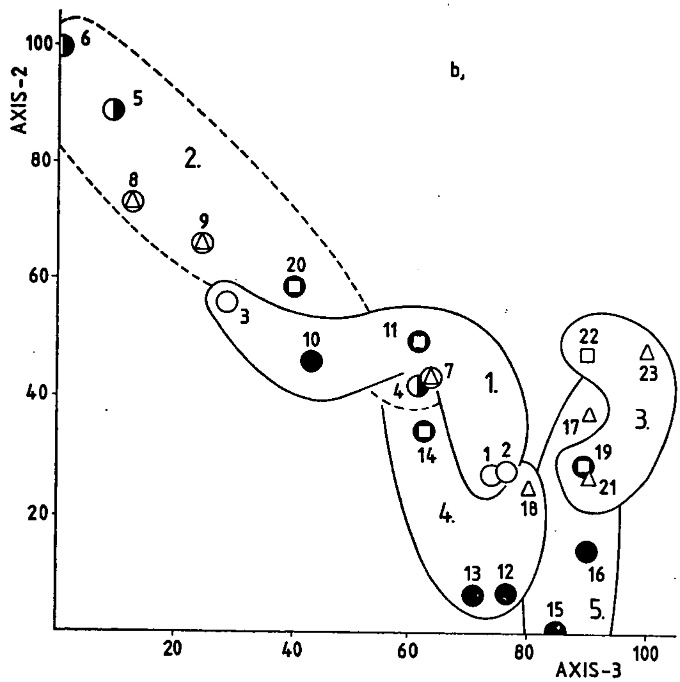
b,
AXIS-2
AXIS-3
2.
1.
3.
4.
5.

Fig. 3.b

analysis (mainly between the 1—3 axes) is ordinated at the area between the two branches. The Nanocyperion elements, with good approach, fall to the same straight line, the equation of which with the transitional elements is as follows:

$$z_{1.ax} = 8.12 - 1.13\ z_{2.ax}$$

The linkage is tight besides the dispersion of r = 0.8510. The Nanocyperion species are situated along the straight line in the sequence of their phenology. First the *Cyperus fuscus* and the *Dichostylis micheliana,* then the *Gnaphalium uliginosum* and the *Veronica anagallis-aquatica* appear in the Nanocyperion associations. The *Rumex stenophyllus* and the *Potentilla supina* reach their highest dominance values in the finishing phase. The relationship between the sequence of appearance and the environmental parameters is shown by the development of the W-indicator value of the species, in due course: 10, 10, 9, 9, 6, 7 (ZÓLYOMI et *al.* 1967). Studying the relationships between the indicator values and the ordination, it could be determined that regularity other than the already mentioned characteristic could not be demonstrated in respect to the location of the species.

Beyond strengthening the results of the cluster analysis, the arrangement of the objects between the 2—3. axes is less informative (Fig. 3b).

Figs. 3c. and 3d. demonstrate the comparison of the cluster analysis with the groups of the ordination. In the case of the 1—3 axes (Fig. 3c) the clusters obtained by the uniting of the complete linkage and the simple average, resp., were segregated, while in the case of the 1—4 axes those clusters were segregated which were obtained from the uniting of the single linkage (Fig. 3d).

Contrary to cluster analysis, the most important, striking advantage of ordina-

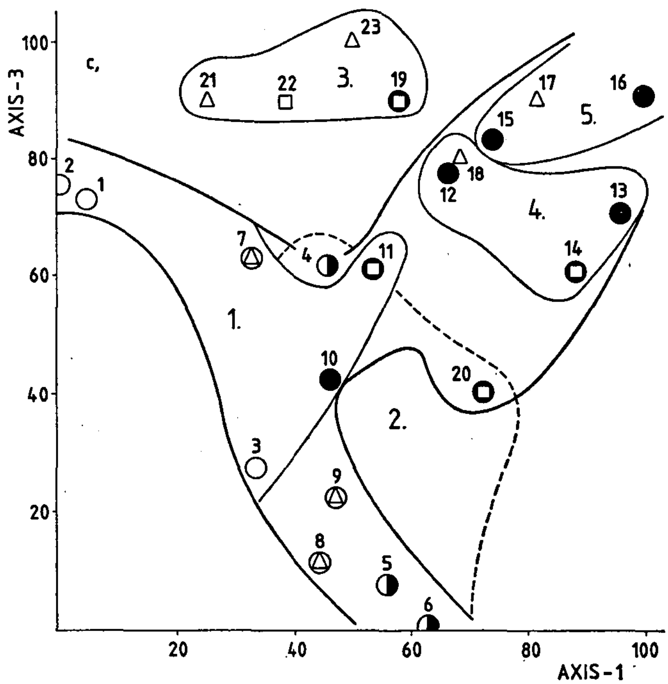

Fig. 3.c

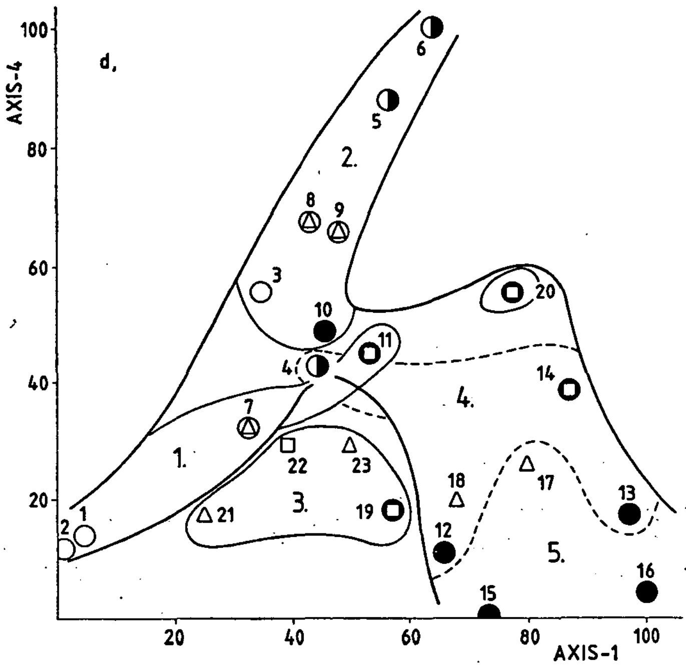

Fig. 3. d

Fig. 3. Results of the reciprocal averaging ordination of species. Detailed interpretation is given in the text. The higher numbers (Fig. b, c, d) indicate the appropriate clusters

tion is that the succession types can be interpreted on the ordination figure. This additional information derives from the dynamic interpretation of the figure, the dynamic character is referred to by the phenological order of succession on the figure of the species belonging to the Nanocyperion group. According to this interpretation the Nanocyperion branch represents the process of the interior primary succession and the Bidentetea branch falling into that of the Nanocyperion represents the process of the exterior primary succession. It is not accidental that the *Chenopodium rubrum,* the character species of the Chenopodion fluviatile association group, was found closest to the Nanocyperion branch. Apart from the major „processes", those species are found the cenosystematic role of which is negligible in respect to the process of both the interior and exterior primary successions (Fig. 3a, 3b).

While the ordination studies reported so far were performed at identical time, providing comparison and evaluation of the various independent relevés, the present study — taking advantage of the possibilities implied in the rapid changes of the Nanocyperion communities — adopts the ordination method to the dynamic system of tightly connected cenoses located at the same area, changing in time and space. As a consequence the quantitative characteristics (e. g. average indicator values) can only be co-ordinated to the different groups of the ordination figure as concomitant phenomena. The ordination of a system or mass of data, which could be regarded as being static, emphasizes the quantitative characteristics, while the main features of a dynamic system are qualitative; the ordination figure lays emphasis on these by the development of the cenosystematical system and the mentioned succession types, resp., as well as by the exact reproduction of the Nanocyperion phenology.

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Vegetációdinamikai vizsgálatok Nanocyperion jellegű cönózisokon II
A fajok klasszifikációja és ordinációja

BAGI I. és KÖRMÖCZI L.

József Attila Tudományegyetem, Növénytani Tanszék, Szeged

Kivonat

A Nanocyperion jellegű cönózisok fajainak reciprocal averaging ordinációs vizsgálatai alapján, a felvételek ordinációjához hasonlóan a folyómeder Nanocyperion zónája benépesülésének kétféle útja különíthető el: interior primer szukcesszió, amely az alacsonyabb térszínekre jellemző és az exterior primer szukcesszió, amely a magasabb térszínekre jellemző folyamat. Az átlagos karakterisztikus indikátorértékek alakulása ezen folyamatok törvényszerű kísérőjelenségeként értékelhető. Az alkalmazott cluster analízis és az ordináció eredményei jól összevethetők. A clusterek kialakulása összefüggést mutat a cönózisok térbeli és időbeli tagolódásával, vagyis a folyómeder iszapnövényzetének vegetációdinamikájával.

Вегетационнодинамическое исследование над растительными сообществами Nanocyperion II.
Классификация и ординация видов

Бали И., Кермеци И.

Университет им. Йожеф А., Кафедра ботаники, Сегед

Резюме

На основании реципровал аверагинг ординантных исследований растительных сообществ Nanocyperion-ного характера, в подобе ординативных приемов в заселении Nanocyperion-ной зоны в речных руслах, где выделяются два путя заселения: интериор пример сукцесивный, который приурочен для более низко расположенного рельефа и экстериор пример сукциесивный — приупочен для более высоко расположенного рельефа.

Образовавшиеся полухарактерные индикаторные результаты в таком случае следует оценивать в процессе закономерных сопровождающих явлений.

Примененный анализ клустера и ординационные результаты здесь хорошо совмещаются. Образование клустеров показывает на взаимные отношения ценозов с территориальным и часовым расчленением, то есть на динамику вегетации иловой растительности.

Ispitivanje dinamike vegetacije sa karakteristikama Nanocyperion zajednice II
Klasifikacija i ordinacija vrsta

BAGI I. i KÖRMÖCZI L.

Katedra za botaniku Univerziteta „József Attila", Szeged

Abstrakt

Na osnovu „reciprocal averaging" ispitivanja vrsta sa karakteristikama Nanocyperion zajednice, slično ordinacijskom snimanju naseljavanja korita reke, uočljiva su dva pravca: interior primer succession koja karakteriše niže slojeve i exterior primer succession karakteristična za više nivoe. Kretanje prosečne karakteristične vrednosti indikatora se javlja kao prateća zakonita karakteristika ovih procesa. Primenjena cluster analiza i rezultati ordinacije se uspešno mogu uporedjivati. Razvoj clauster-a pokazuje povezanost izmedju vremenske i prostorne diferencijacije zajednica, odnosno sa dinamikom vegetacije flore mulja u koritu reke.