COMPARATIVE ANALYSIS OF SUCCESSIONAL STAGES OF SANDY VEGETATION - A CASE STUDY

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Abstract. The vegetation of seven selected sites, representing different stages of primary succession, is analyzed in order to establish a feasible successional scheme, and to compare the traditional successional pathways and the pathway suggested by the multivariate methods.
The ordination of micro-scale coenological relevés suggests a more or less linear successional sequence of studied stands corresponding with the traditional theory.
Five typical patches were identified in each stand by classification in order to represent the internal variability of the vegetation. Ordination of these typical patches on the basis of species frequencies shows, that the primary dynamic of the sand vegetation is more complex. The linear successional sequence of studied stands is unlikely, different transitions between stages are equiprobable, and the graph structure of series is rather reticular.
Three groups of stands were identified by diversity ordering: (i) an initial, open grassland type with low diversity; (ii) a grassland with medium diversity ; the forest herb layer also belongs to this category; (iii) the most diverse, closed grassland, and the shrubby habitat. Diversity profiles of these groups were clearly separated.
The methods employed differentiate the vegetation of the studied stands according to their species composition, diversity and complexity, but the established sequence does not necessarily reflect to the real historical development of the stands in question.

Keywords: sandy vegetation, succession, multivariate methods, diversity ordering

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Introduction

One of the typical vegetation and flora types of the Hungarian Plain can be found on sandy areas between the Danube and Tisza rivers. This vegetation has been studied by many authors, among them such pioneers as Kerner (1863) and Rapaics (1918). The successional stages were described by Hargitai (1940), Zsolt (1943) and Magyar (1960). Besides this classical works, Précsényi (1981) studied the diversity changes during succession and there are several publications elucidating certain ecophysiological phenomena of such vegetation (e.g. Tuba, 1984 and Fekete et al., 1988). The spatial pattern as well as the niche relations of some species belonging to the grassland community *Festucetum vaginatae* were studied by Molnár and Nosek (1979) and Fekete et al. (1980).

Recently Fekete (1992) published a new concept of primary succession, wich is different from the traditional interpretation by the Hungarian phytosociologists. He pointed out that the primary dynamics of sandy vegetation is very complex: the vegetation-soil evolution is non-parallel; the succession is often determined by stochastic transitions between stages; the successional graph structure of the sand sere is rather reticular than linear; origin of climax stage is heterogeneous. The pioneer grassland does not accumulate sufficient humus for the establishment of steppe-meadow species, so the steppe meadow does not fit the pioneer grassland-shrub line. The stands of oak wood (the climax community in the traditional concept) are habitat-dependent.

Although the classical phytocoenological description of sandy vegetation succession is given in the above mentioned papers, no detailed multivariate analysis has been made to describe vegetation differences among the stages.

Classifications and ordinations are suitable for analysis of succession, but the effectiveness of different methods depends on the nature of analyzed data (Mazzoleni, 1991).

Unequivocal successional sequences are not necessarily self evident to critical observer (Anderson, 1986). For example, computer based classification and ordination techniques defined a successional gradient that differed from a theoretical or assumed successional classification in the case of a big sagebrush/grass community (Tueller and Platou, 1991).

The aim of this study is to analyze the vegetation of selected habitats in a Hungarian sandy area using multivariate methods and diversity comparisons, and to evaluate the different concepts of succession according to the results.

The ant community composition and epigeic fauna of the same study plots analysed in this paper has also been studied (Járdán et al., 1993).

Study area and Methods

1. Site description

The field studies were carried out in a nature reserve in the southern part of Hungary, between the rivers, Duna and Tisza near to the village Kéleshalom in June 1991. The study site is a complex of wind-blown sand dunes. Several successional stages of sandy vegetation occur here from bare sand to poplar forest. For the present study 7 plots were selected, representing these stages:

Plot 1. Almost bare sand with some plant species belonging to the association *Festucetum vaginatae*. The bare surface within the plot may derive from an abandoned sand-mine.

Plot 2. Open perennial grassland with 30-40 % plant coverage, predominating by *Festuca vaginata* (*Festucetum vaginatae danubiale*). The moss and lichen layer was also considerable.

Plot 3. Similar to plot 2, but predominated by *Stipa borysthenica*. (*Festucetum vaginatae stipetosum borysthenicae*)

Plot 4. Open perennial grassland predominated by the species belonging to the *Festucetum vaginatae* community and *Populus alba* forms a shrub storey here. Height of it is 50 cm, about 25 % cover).

Plot 5. Closed grassland with some xeromesophilous and mesophilous species besides the xerotolerant ones. The phytocoenological status of this stand is uncertain.

Plot 6. Shrubby habitat with 50-60 % coverage of *Crataegus monogyna, Juniperus communis, Berberis vulgaris* and *Ligustrum vulgare* shrubs

Plot 7. Closed poplar (*Populus alba*) forest with some *Robinia pseudoacacia* trees. *Crataegus monogyna* and *Juniperus communis* give a sparse shrub layer.

The areas of the study plots were about 400 m^2.

2. Field sampling

A similar sampling procedure was applied than described by Szollát and Bartha (1991) with some modifications. Long transect of 200 contagious small plots, each of 20x20 cm size, were used for sampling in each stand. The total transect of 40 m lenght was broken 4-5 times, resulting a zig-zag line "netting" the whole plot. The presence and absence of species rooting in the subplots were recorded. In the shrubby habitat and in the poplar forest only the herb layer was sampled. The presence of detectable lichen and moss species were recorded and analysed together with the higher plants.

3. Data analysis

The seven study sites were ordinated according to the pooled frequency of occurring species using principal coordinate analysis with Czekanowski index by the program package NuCoSA (Tóthmérész, 1991, 1993a). Virágh (1986) havs found the same ordination method and similarity index to be useful for detecting vegetation differences in a similar scale study.

In order to represent the internal variability of the stands five most abundant characteristic patch types (10 contagious 20x20 cm subplot of each) were selected in each stand by classification of all 200 subplots according to their species composition, using the Sørensen similarity index by the NCLAS2 program of SYN-TAX III. program package (Podani, 1988). These 20x100 cm^2 subplots, representing typical patches, were classificated by NuCoSA using Czekanowski similarity index and single linkage sorting algorithm. Principal coordinate analyses (NuCoSA) of the same subplots were performed using again Czekanowski index, and the results of clustering method and ordination were combined.

Analysis of the diversity conditions were performed by diversity ordering (Tóthmérész 1993a,b). This evaluation differentiates the diversity sequence of studied communities based on dominant versus rare species. The Hill diversity value is sensitive on rare species at low scale parameter value and it is sensitive on dominant species at high parameter value.

Table 1. The pooled frequency values of the species in the 200 20x20 cm quadrate per study plot. Data of 22 rare species, whose pooled frequency values were below 10 are not indicated. The used nomenclature is after Simon (1992).

SPECIES	STUDY PLOTS						
	1	2	3	4	5	6	7
Achillea pannonica	0	0	0	0	11	72	0
Alyssum tortuosum	30	1	5	39	0	0	0
Asclepias syriaca	16	0	0	0	0	0	0
Asperula cynanchyca	0	0	0	0	0	27	0
Berberis vulgaris	0	0	0	0	0	26	27
Botriochloa ischemum	0	0	9	9	0	0	0
Bromus sterilis	0	0	0	0	0	0	36
Calamagrostis epigeios	0	0	0	0	16	4	0
Camptothecium lutescens	0	0	0	0	0	54	0
Carex flacca	0	0	0	0	0	0	72
Carex liparicarpos	12	24	34	77	58	119	127
Cladonia convoluta	0	59	8	4	1	0	0
Cladonia magyarica	0	33	0	0	14	0	0
Cladonia rangiformis	0	0	0	0	8	56	0
Cornus sanguinea	0	0	0	0	0	19	10
Crataegus monogyna	1	0	0	0	0	9	36
Cynodon dactylon	0	0	14	0	0	0	2
Cynoglossum officinale	0	0	0	32	0	0	0
Equisetum ramosissimum	0	0	0	0	26	0	0
Erigeron canadensis	1	13	0	4	0	0	0
Erysimum diffusum	0	4	5	7	3	0	0
Euphorbia cyparissias	0	2	0	0	6	23	0
Euphorbia segueriana	59	12	29	10	2	9	0
Falcaria vulgaris	0	0	0	0	0	14	0
Festuca vaginata	124	109	68	167	22	45	5
Festuca wagneri	0	0	0	0	73	18	0
Fumana procumbens	17	5	70	3	0	0	0
Galium verum	0	0	0	0	94	37	4
Holoschoenus romanus	0	0	0	0	42	0	0
Kochia laniflora	0	30	66	4	9	0	0
Koeleria glauca	12	13	36	0	2	4	0
Ligustrum vulgare	0	0	0	0	0	24	55
Minuartia glomerata0	4	0	8	0	0	0	
Minuartia verna	5	28	8	0	1	2	0
Parmelia pokornyi	0	39	58	2	1	0	0
Pimpinella saxifraga	0	0	0	0	0	0	10
Pleurochaete squarrosa	0	36	0	0	37	7	0
Poa angustifolia	0	0	0	0	43	51	12
Polygonum arenarium	0	7	5	50	12	0	0
Populus alba	0	0	0	33	0	0	0
Potentilla arenaria	0	37	18	16	23	76	0
Prunus spinosa	0	0	0	0	0	2	27
Scabiosa ochroleuca	0	0	0	0	21	55	0
Sedum hillebrandtii	0	3	11	0	0	0	0
Stipa borysthenica	23	132	105	61	51	98	0
Stipa capillata0	0	0	0	64	0	0	
Syntrichia ruralis	5	70	16	34	22	0	0
Taraxacum officinale	0	0	0	0	1	5	4
Teucrium chamaedrys	0	47	0	0	113	26	48
Thesium arvense0	0	0	0	4	6	0	
Thymus pannonicus	15	46	45	0	52	101	0
Torilis japonica	0	0	0	0	0	0	16
Viola rupestris	0	0	0	0	0	32	5
Total species number	15	24	21	19	35	33	28

Result

Ordination and classification of study plots

The ordination of the seven stands according to the pooled frequency of occurring species defined a successional sequence, that did not differ considerably from a theoretical or assumed successional order, if the arch effect of the ordination method is taken into consideration; only the plot 4 does not fit well into the sequence (Fig. 1.).

The selected representative subplots of the stands were separated rather well on the PCoA scattergram (Fig. 2.), and the classification results confirm the togetherness of these subplots (Fig. 3.). There are very few overlaps between the different stands, consequently between the successional stages. Only the subplots of the shrubby habitat (plot 6) form no separate cluster and they are positioned far from each other on the central part of the scattergram. The vegetation of this stand is very heterogeneous. The identified patch types may represent different successional stages, and can be ordered in a feasible successional sequence that is parallel with the sequence of the other stands (Fig. 2.).

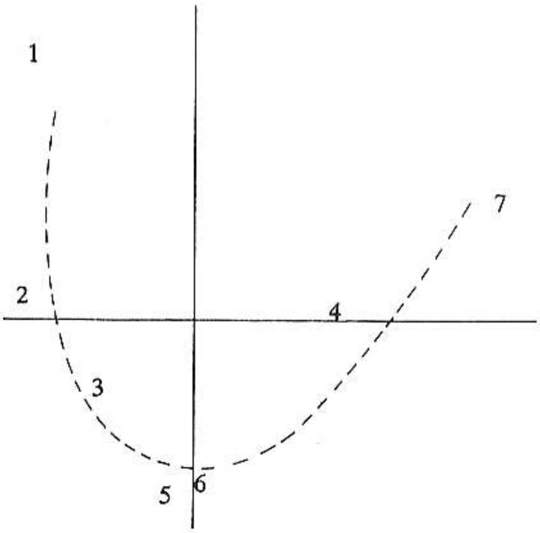

Fig. 1. Principal coordinate analysis of the study plots according to the pooled frequencies of the occurring species. For the description of the study plots indicated by numbers see the "Study area and Methods".

Some subplots do not join to any group; they represent unical patch types. On Fig. 2. the subplots of plot 1. and plot 4. are encircled together, this two plots represent the initial stage of succession in this area. Inside the denoted cluster the two study sites are separated (Fig 3.).

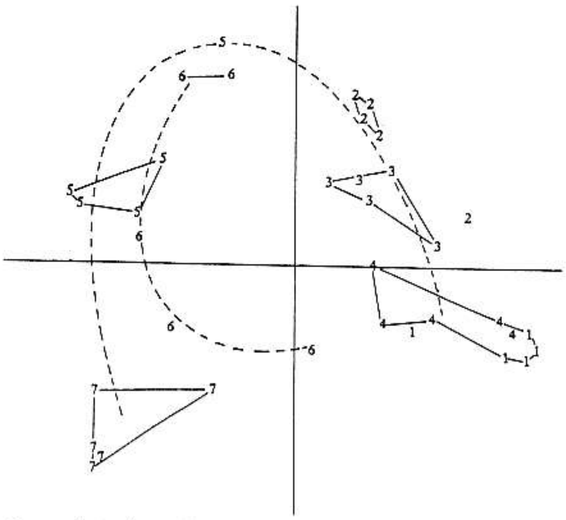

Fig. 2. Principal coordinate analysis of the representative subplots of the studied stands. Lines encircle the subplots belonging to the same cluster, indicated by stars in Fig. 3. The dashed lines sign possible orders of the samples considering the arch effect of the ordination method.

Diversity

Altogether 76 species were recorded in the 7 stands. The frequencies of species are presented on Table 1. (Data of 22 rare species, whose summed frequency values were below 10 are not indicated.)

Three groups of stands were identified by diversity ordering: (i) an initial, open grassland type with low diversity; (ii) a grassland with medium diversity; the forest herb layer also belongs to this category; (iii) the most diverse, closed grassland, and the shrubby habitat. Diversity profiles of these groups were clearly separated.

In the first group the diversity of plot 1 is unambiguously lower, than that of the plot 4. However in the medium diversity group the profile of plots 2, 3 and 7 cross each other, this means that these three communities cannot be ordered simply by their diversity. At lower scale parameter, that is, regarding the rare species the diversity of the plot 7 is the highest, but the opposite is right at the higher value of scale parameter -- regarding the dominant species.

Discussion

According to the traditional interpretations (Zsolt, 1943 and Magyar, 1960) the feasible successional sequence of studied stands is the

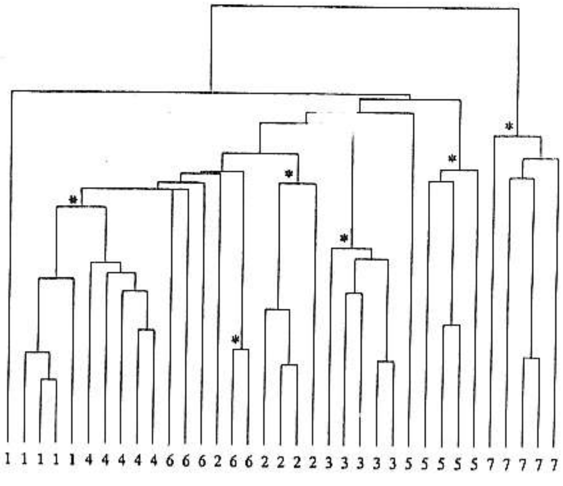

Fig. 3. Dendrogram of the representative subplots of the studied stands. The stars indicate the relevant clusters, subplots of which are encircled by lines in the ordination diagram in the Fig. 2.

following: almost bare sand (plot 1) -- *Festucetum vaginatae danubiale* (plot 2) -- *Festucetum vaginatae stipetosum sabulosae* (plot 3) -- open grassland with small poplar trees (plot 4) -- closed grassland (plot 5) -- shrubby habitat (plot 6) -- poplar forest (plot 7). On the PCoA scattergram of stands this sequence can be more or less recognized if considering the arch effect of the ordination method (Fig.1.). The arch effect is stronger when the ordinated samples have few species in common (Mazzoleni et al., 1991). The *Brometum tectorum*

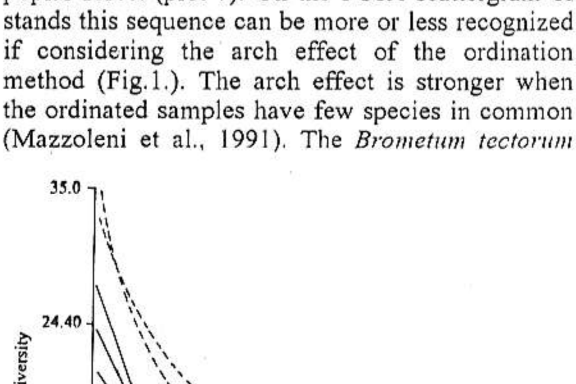

Fig 4. Diversity ordering of the study plots, according to the pooled frequency values of the occurring species. For description of the study plots indicated by numbers see the "Study area and Methods".

community, an annual grassland, which is regarded by the traditional concept as the first stage of sandy succession cannot be found in Kéleshalom site. *Festuca vaginata* is the most frequent species in the very open, presumably pioneer stages (plot 1 and plot 4). It is remarkable, that poplar can colonize even in the very initial form of *Festucetum vaginatae* community the (plot 4).

Fekete (1992) presented a different concept of primary succession on sand: the starting point is usually *Festucetum vaginatae* community. The succession terminates at the *Junipero - Populetum* along many lines; this community corresponds to the real forests in this sere. The steppe meadow (closed grassland) does not fit to the pioneer grassland -- shrub line and this makes the graph reticulated in this xeroseries.

The result of analysis reflecting to the internal variability of the stands (Fig. 2.) support this concept rather than the traditional, linear successional sequence. The starting point is undoubtedly the complex of the plot 1 and plot 4; plot 2, 3, 5 and 7 could be alternative endpoints of succession. Besides this an alternative explanation of the scattergram is also possible: (1-4) -- 3 - 2 - 5 - 7 plot sequence could be recognized along an arch in the Fig. 2.

The subplots of plot 6 may represent intermediate stages of alternative pathways leading from the open grassland (plot 1,4) to the closed grassland (plot 5) and poplar forest (plot 7). At the same time the subplots representing typical patches of plot 6 are ordered along an arch, parallel with the mentioned (1-4) -- 3 - 2 - 5 - 7 plot sequence in the scattergram. That is, alternative interpretations are possible when trying to identify the successional sequence on the base of the ordination result. The used methods are suitable to arrange the communities according to their complexity, and species composition but it does not mean, that the identified sequence exactly corresponds to the real historical development of the stands in question.

In a hilly area there are considerable differences in the physico-chemical condition of the soil (i.e., humus and nitrogen content, water content and soil granule size) at the top of the sand hills, in the wind grooves between them and at the relatively flat areas (Körmöczi, 1983). Such environmental differences may cause the development of alternative endpoints of succession, according to the concept of Drake (1990), who regard the environmental gradients as a filter defining which set of species is permissible to colonize.

The species diversity is the highest in the closed grassland (plot 5) and in the shrubby habitat (plot

6), but presumable because of different reasons. In the case of closed grassland community the more favourable environmental conditions of the slight wind grove habitat (higher soil humidity, lower wind effect and insolation) allow the coexistence of more species. The shrubby habitats have developed in the upper slope of a sand hill, and the shrubs stand separately providing a wide variety of microhabitats from the open, dry patches between the shrubs to the shaded sites under their canopy, were the soil is covered by litter. Here the habitat heterogeneity causes higher number of species.

Studying similar sandy vegetation Précsényi (1981) found that the species diversity was the lowest in the last stage of succession, that is in the forest. In present case the diversity of forest herb layer is high if regarding the rare species, but considerably lower if regarding the dominant species (Fig. 4.). This community does not evolve automatically from a previous grassland stage, but the light shortage (the shading effect of the growing tree canopy) drives its development. So, because of the considerable change in environmental conditions a different species pool is allowed to colonize (cf. Drake, 1990)

The vegetation of plot 4 provides an evidence, that the reforestation of open grassland is possible, but cannot be found clear transitional stages between the open grassland and forest herb layer among the studied plots.

Present paper refers to field investigations of one single time point. Direct evideces about the successional pathways can be drawn up only after several years study period on permanent plots. Result of such a long term study carried out on the vegetation of Hungarian sandy areas have not been published yet. Although better understanding of the succession is very important from the nature conservation point of wiev as well, because the conservation activity have to aim at maintainance of all succesional stages close to each other if it is possible. But the minimal spatial scale of the successional processes is not known yet as well.

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