

INTERSPECIFIC ASSOCIATIONS IN DIFFERENT SUCCESSIONAL STAGES OF THE VEGETATION IN A HUNGARIAN SANDY AREA

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Abstract. Intraspecific associations were studied in seven plant communities in a Hungarian sandy area. Aim of present study was to reveal the differences of species coexistence structures in the vegetation of different successional stages.

The frequency and intensity of pairwise interspecific associations positively correlated with the species number. It was proved, that the higher association value was not only a statistical consequence of higher species number in the species rich stands, but it referred to the organization degree of studied communities, because the species association values of the real, field samples were considerable higher than that of the spatially randomized reference of the same data.

The value of the community level measure 'associatum' and sum of the pairwise associations show similar rank of the studied stands. Both measures were spatial scale dependent.

Combination of principal coordinate analysis and plexus diagram method indicated two coalitions in the species rich communities, such as closed grassland and shrubby habitat: an assemblage with higher species number and a second one with lower species number.

Keywords: interspecific association, associatum, information theory statistics, spatial scale dependence, succession, sandy vegetation

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Introduction

The frequency and intensity of interspecific spatial associations belong to the most widely used measures of coexistence and interaction in plant communities. Usually a strong positive association can be obtained between species belonging to the same community (Greig-Smith, 1983).

Association analysis is especially useful to gain insight into the mechanisms of successional processes. Recently, the role and importance of interspecific association in succession were studied by several authors. Kikvidze (1992) demonstrated, that the selection of species composition is going on through the 'sieve' of interspecific relations during succession of alpine-subnival vegetation patches.

No consistent trend was found in changes of the frequency of significant associations when several stages of old-field succession were compared (Leps and Burianek, 1990).

The proportion, number, and level of significance of interspecific associations declined in

ten old fields during 31 years of succession (Myster and Pickett, 1992). Moderate cattle grazing decreased the number of both positive and negative associations in a grassland community (Matus and Tóthmérész, 1990).

The above-mentioned studies dealt with pairwise associations of species. Studying ecological coalitions, that is organization between population and community level, has central importance in understanding species coexistence in plant communities. Matejka (1992) specified two units in this organization level - microcoenosis (a spatial unit), and structural group of species (similar to the notion of coalition). Vegetation should be viewed as a mosaic of species combinations, rather than separate species patterns (Bartha, 1992).

The plant communities representing different successional stages form a landscape-level mosaic-like pattern on sandy areas of the Hungarian Plain. Possible successional sequences of them were described by Hargitai (1940), Zsolt (1943) and Magyar (1960). Recently Fekete (1992) published a

new concept of primary succession of sandy vegetation which differs from the traditional interpretation of the Hungarian phytosociologists.

Interspecific association of species was used for examining ecological specialization in a grassland community called *Festucetum vaginatae* (Rapaics, 23) Soó 29 by Précsényi et al. (1980), but the change of interspecific association relations during succession of this type of vegetation have not been analyzed.

The aim of present study was to investigate the change of species coexistence structure and interspecific association relations as a function of succession within sand vegetation.

Précsényi (1981) and Margóczy (1993) demonstrated species diversity changes during succession of sandy vegetation. The higher the species number, evidently, the higher the frequency of possible pairwise association of species, if the relative frequency of species is balanced. In this study I investigated, whether the increase of intensity and frequency of pairwise association during succession is just a result of higher species number, or this increase refers to other elements of complexity of the studied communities.

Study area and methods

Site description

The field studies were carried out in a nature reserve situated in the southern Hungary, between the rivers Danube and Tisza near the village of Kéleshalom. The study site is a complex of wind-formed sand dunes. Several successional stages of sand vegetation ranging from bare sand to poplar forest occur at the site. For the present purposes 7 plots were selected, which represent the following stages:

Plot 1: **sparse, pioneer vegetation** with some plant species typical of the *Festucetum vaginatae*; the bare surface within the plot may derive from an abandoned small sand-mine.

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

Plot 3: similar to Plot 2, but predominated by *Stipa borysthena* (*Festucetum vaginatae danubiale stipetosum borysthena*).

Plot 4: open perennial grassland predominated by species of the *Festucetum vaginatae*. **Populus**

alba forms a shrub storey here. (50 cm in height, about 25 % in cover).

Plot 5: **closed grassland** with some xero-mesophilous and mesophilous species besides the drought-tolerant ones.

Plot 6: **shrubby habitat** (50-60 % cover) of *Crataegus monogyna*, *Juniperus communis*, *Berberis vulgaris* and *Ligustrum vulgare*.

Plot 7: closed **poplar (*Populus alba*) forest** with admixed *Robinia pseudoacacia* trees; *Crataegus monogyna* and *Juniperus communis* make a sparse shrub layer.

The areas of the study plots were about 400 m². The vegetation of these plots was studied by Margóczy (1993) using multivariate analysis. Ant assemblages and epigeic fauna of the same study sites were studied by Járdán et al. (1993).

Field sampling

We used a modified version of the sampling procedure developed by Szollát and Bartha (1991). Long transects of 200 contiguous small plots, each sized 20 x 20 cm, were sampled in each stand. The 40 m long transect was folded 4-5 times, resulting a zigzag line "netting" the whole plot. The presence of species rooting in the subplots was recorded. In the shrubby habitat and in the poplar forest only the herb layer was sampled. The presence of lichen and moss species was recorded and analyzed with the higher plants.

Data analysis

Pairwise associations of species were computed from the 2 x 2 contingency tables of each species pair. Zarr (1984) recommend to use G test for analyzing contingency table data, where

$$G = 2[m \log m + a \log a + b \log b + c \log c + d \log d - (a+c) \log (a+c) - (b+d) \log (b+d) - (a+b) \log (a+b) - (c+d) \log (c+d)]$$

a, b, c, and d correspond to the notations of a 2x2 contingency table, m=a+b+c+d is sample size.

The same formula was used to define pairwise association of species by Juhász-Nagy and Podani (1983) as one of the functions of information theory method for the study of spatial processes and succession. In their paper, the formula of pairwise association is as follows

$$mI(A,B) = G/2$$

Table 1. Frequency values of the species in the 200 20x20 cm subplots per study plot. Data of 22 rare species, whose pooled frequency values were below 10 (i.e. 5 %) are not indicated. The used nomenclature is after Simon (1992).

SPECIES	STUDY PLOTS							CODE
	1	2	3	4	5	6	7	
Achillea pannonica	0	0	0	11	72	0	0	ACHI
Alyssum tortuosum	30	1	5	0	0	39	0	ALYS
Asclepias syriaca	16	0	0	0	0	0	0	ASCL
Asperula cynanchyca	0	0	0	0	27	0	0	ASPE
Berberis vulgaris	0	0	0	0	26	0	27	BERB
Botriochloa ischemum	0	0	9	0	0	9	0	BOTR
Bromus sterilis	0	0	0	0	0	0	36	BROM
Calamagrostis epigeios	0	0	0	16	4	0	0	CALAM
Camptothecium lutescens	0	0	0	0	54	0	0	CAMT
Carex flacca	0	0	0	0	0	0	72	CAFL
Carex liparicarpos	12	24	34	58	119	77	127	CARE
Cladonia magyarica	0	33	0	14	0	0	0	CLMA
Cladonia rangiformis	0	0	0	8	56	0	0	CLRA
Cladonia convoluta	0	59	8	1	0	4	0	CLCO
Cladonia furcata	0	39	58	1	0	2	0	CLFU
Cornus sanguinea	0	0	0	0	19	0	10	CORN
Crataegus monogyna	1	0	0	0	9	0	36	CRAT
Cynodon dactylon	0	0	14	0	0	0	2	CYNO
Cynoglossum officinale	0	0	0	0	0	32	0	CYOF
Equisetum ramosissimum	0	0	0	26	0	0	0	EQUI
Erigeron canadensis	1	13	0	0	0	4	0	ERIG
Erysimum diffusum	0	4	5	3	0	7	0	ERYS
Euphorbia cyparissias	0	2	0	6	23	0	0	EUPH
Euphorbia seguieriana	59	12	29	2	9	10	0	EUPH
Falcaria vulgaris	0	0	0	0	14	0	0	FALC
Festuca wagneri	0	0	0	73	18	0	0	FEWA
Festuca vaginata	124	109	68	22	45	167	5	FEVA
Fumana procumbens	17	5	70	0	0	3	0	FUMA
Galium verum	0	0	0	94	37	0	4	GAVE
Holoschoenus romanus	0	0	0	42	0	0	0	HOLO
Kochia laniflora	0	30	66	9	0	4	0	KOCH
Koeleria glauca	12	13	36	2	4	0	0	KOEL
Ligustrum vulgare	0	0	0	0	24	0	55	LIGU
Minuartia glomerata	0	4	0	0	0	8	0	MIGL
Minuartia verna	5	28	8	1	2	0	0	MINU
Pimpinella saxifraga	0	0	0	0	0	0	10	PIMP
Pleurochaete squarrosa	0	36	0	37	7	0	0	PLEU
Poa angustifolia	0	0	0	43	51	0	12	POAN
Polygonum arenarium	0	7	5	12	0	50	0	POAR
Populus alba	0	0	0	33	0	0	0	POPU
Potentilla arenaria	0	37	18	16	23	76	0	POTE
Prunus spinosa	0	0	0	0	0	2	27	PRUN
Scabiosa ochroleuca	0	0	0	0	21	55	0	SCAB
Sedum hillebrandtii	0	3	11	0	0	0	0	SEDU
Stipa borysthena	23	132	105	61	51	98	0	STBO
Stipa capillata	0	0	0	0	64	0	0	STCA
Syntrichia ruralis	5	70	16	34	22	0	0	SYNT
Taraxacum officinale	0	0	0	0	1	5	4	TARA
Teucrium chamaedrys	0	47	0	0	113	26	48	TEUC
Thesium arvense	0	0	0	0	4	6	0	THES
Thymus pannonicus	15	46	45	0	52	101	0	THYM
Torilis japonica	0	0	0	0	0	0	16	TORI
Viola rupestris	0	0	0	0	0	32	5	VIOL
SPECIES NUMBER	16	24	21	19	35	35	28	

The higher this value the greater is the information obtained on species B by determining the score for species A and vice versa. The pairwise association values [mI(A,B)] were computed for each 7 site

separately, by the program INPRO3 of the program package SYN-TAX III. (Podani, 1988).

The significant positive pairwise association values were indicated by edges in the principal

coordinate analysis (PCoA) scattergram of species computed by the program PRINCOOR from SYN-TAX III., Jaccard similarity was used as the resemblance measure. Since G is approximately distributed as χ^2 , and the degree of freedom is 1 in the case of 2 x 2 contingency table (Zarr, 1984) $\chi^2=3.841$ ($P=10\%$) was used as an arbitrary threshold for connecting species by edges. Combination of association analysis, and PCoA is very similar to the plexus graph method used by Matus and Tóthmérész (1991). This method was used to reveal the coalition structure of the studied communities.

Associatum is an other important function of the information theory method (Juhász-Nagy, 1976). It is a community level measure that refers not only to the pairwise interspecific association relations, but it is a quantitative expression of the spatial dependence of the realized species combinations. Description of the method and formula of associatum are given in Juhász-Nagy and Podani 1983.

Since the size of the sample plots influences the probability of finding a given species combination (Juhász-Nagy and Podani, 1983; Szollát and Bartha, 1991) the sum of positive pairwise association values and associatum of each study site were computed at 15 different sampling unit sizes. The different plot sizes were obtained by combining 2, 3, 4, 6, 8, 10, 14, 18, 22, 26, 30, 34, 38, and 50 20x20 cm subplots by the program Spat-Proc (Horváth, unpublished).

The same data analysis was performed on random data matrices, and the results were compared with the real, field situation. Original matrices, containing the species presence data in the subplots were rearranged in order to gain random reference. The presence of species in the subplots was spatially randomized, without any change of the original species numbers and frequencies in the complete data set. The spatial dependence of species association measures counted from real and random data is displayed on the Fig. 4 in the case of an open grassland (Plot 2) and the closed grassland (Plot 5).

The species association measures were plotted against species number in the case of field data and their random reference. The used spatial scale was that where the departure from random reference was considerable at both measures (plot size 20x160 cm).

The Shannon diversity values of the 7 study sites were computed from the frequency values of species in the 200 subplots, species number is shown in Table 1.

Results

Diversity and species associations

Altogether 53 species were detected in the 7

study sites. The frequency data of species are presented in Table 1. Data of 22 rare species, pooled frequency values of which were below 10 (i.e. below 1%) are not indicated.

The diversity values of the study sites are shown in Fig. 1. Diversity and species number is high in the closed grassland (plot 5.) and in the shrubby habitat (Plot 6), low in bare sand (Plot 1) and in the open grassland with small poplar trees (Plot 4). (Fig. 1.)

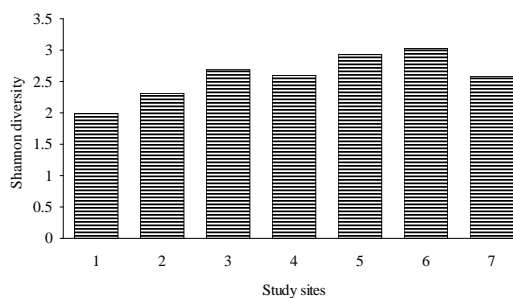


Fig. 1. Shannon diversity values of the study sites computed from the species frequencies given in Table 1.

The rank order of the sample sites is rather similar according to the sum of positive pairwise associations, associatum (maximal values), species number and diversity (Table 2), indicating the positive correlation between these measures. The question is, whether the frequency and intensity of species association is only a statistical consequence of species number, or it also refers to the complexity of the studied communities as well.

Table 2. The rank order of the sample sites according to the species number, diversity, maximal values of the sum of positive pairwise associations and associatum.

Species number	1 < 4 < 3 < 2 < 7 < 6 < 5
Diversity	1 < 2 < 7 < 4 < 3 < 5 < 6
Sum of positive pairwise associations	1 < 3 < 2 < 4 < 7 < 6 < 5
Associatum	1 < 4 < 3 < 2 < 7 < 5 < 6

The sum of positive associations showed spatial scale dependence (Fig. 2). They reach maximal values at relatively large plot sizes, between 360x20 and 1000x20 cm. These values are considerably higher than the association values found for the 20x20 cm plot size, but the rank of the studied stands is rather similar. Three categories can be differentiated in both cases: Low, Medium and High intensity association levels. The sparse, pioneer vegetation of the Plot 1. represents the Low association level category, the two open grasslands (Plots 2 and 3) the Medium one, the closed grassland and shrubby habitat (Plots 5 and 6) the High association level category. The relative difference

between the maximal association intensity and the value found for the 20x20 cm spatial scale is higher in the case of the open grassland with small poplar trees (Plot 4) and the forest grass layer (Plot 7). Therefore Plot 4 belongs to the Low level association category at 20x20 cm sample size, but to the Medium level category regarding the maximal values. The Plot 7 belongs to the Medium level association category at 20x20 cm sample size, but to the High level category regarding the maximal values (Fig. 2).

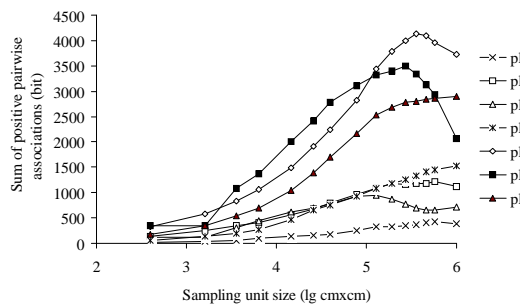


Fig. 2. Spatial scale dependence of the sum of positive pairwise species associations.

The associatum showed spatial scale dependence as well (Fig. 3.). The rank of the study sites on the basis of associatum values were rather similar, than in the case of pairwise associations both at 20x20 cm sampling unit size and at maximal values.

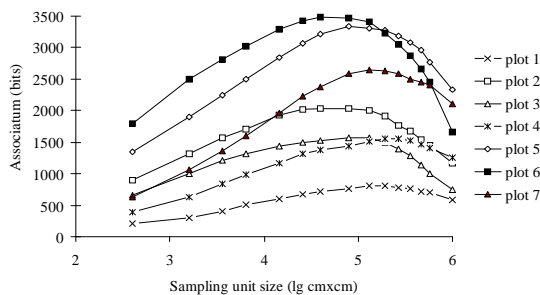


Fig. 3. Spatial scale dependence of associatum.

Departure from the random reference

The spatial dependence of the departure was displayed in the case of an open grassland (Plot 2) and the closed grassland (Plot 5) (Fig. 4). Difference between the sum of positive pairwise associations, and associatum values of the real and random data were considerable high at larger spatial scales.

A positive correlation was found when the species association measures were plotted against the species number (Fig. 5). The increase of species association frequency and intensity with species number was much more intensive in the case of field

data than that of their random reference.

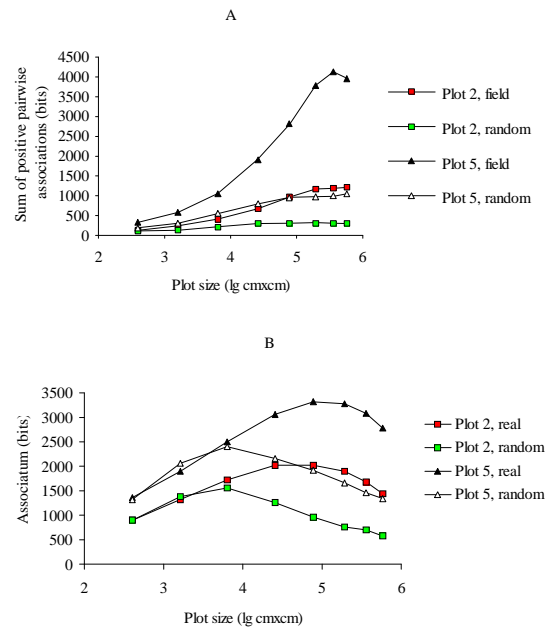


Fig. 4. Spatial scale dependence of the sum of positive pairwise associations (A) and associatum (B) in real, field situation, and in the spatially randomized case.

Ordination of species and possible coalition structure

In the study site of pioneer, sparse grassland (Plot 1) no intensive positive association developed between the frequent species. This community is very simple and undeveloped, represents the pioneer stage of sandy succession. Only two pairs of species are associated in the open grassland with small poplar trees (Plot 4). So, plexus graphs of these two study sites are not shown.

The frequency of associations is higher in the two open grassland study sites (Plot 2 and 3), and the coalition structure is rather similar (Figs. 6 and 7). Two separate coalitions exist, one with four members and an other with three members in both stands. A parallel feature is, that PARM (a lichen species) is a central member in the three-member group, and the other member (THYM in Plot 2, and POTE in Plot 3) has similar growing form. Clonal growth along the soil surface is characteristic on both species. The KOCH is a member of the four-member coalition, but it is difficult to find out any possible assembly rule, for the other three members has rather different character in Plot 2 and 3. The dominant perennial grasses (FEVA and STBO) are close to each other in the graph, but do not belong to any coalition, perhaps because of their high frequency (they are present in almost every subplots).

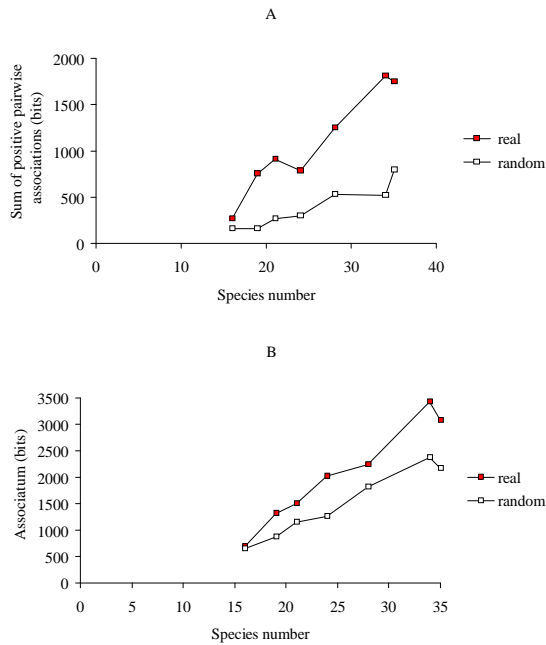


Fig. 5. Connection between the species number and the sum of positive pairwise associations (A), and associatum (B), computed from the real, field data matrices and from their spatially randomized references.

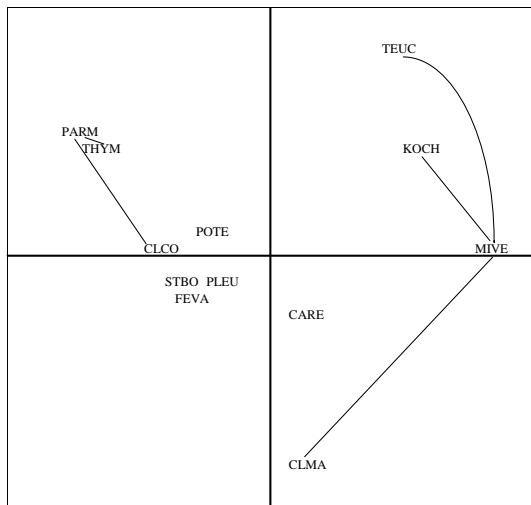


Fig. 6. Plexus graph of the species of Plot 2. The species are arranged according to the first two axis of the PCoA, Czekanowski similarity was used as the resemblance measure, plot size: 20x160 cm. The significant positive pairwise association values are indicated by edges. The species below 5% frequency value are not shown. Species names belonging to the abbreviations are given in Table 1.

In the closed grassland (Plot 5) and in the shrubby habitat (Plot 6) there are more significant associations (Figs. 8 and 9). Two coalitions can be separated in both plots: a dominant one containing

more species, and a subordinated coalition with fewer members. The dominant coalition in Plot 5 include 9 species with rather mesophilous and generalist character. The subordinated coalition is represented here by *Stipa borysthena*, two *Festuca* species and a moss (*Syntrichia ruralis*). These species belong to the open sand grassland community (*Festucetum vaginatae*) which has a drought tolerant character.

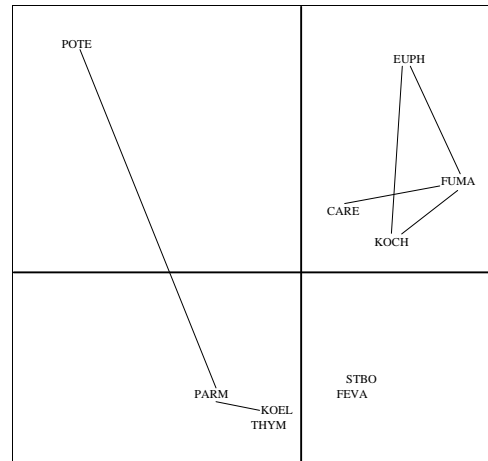


Fig. 7. Plexus graph of the species of Plot 3. (Details are given at Fig. 6).

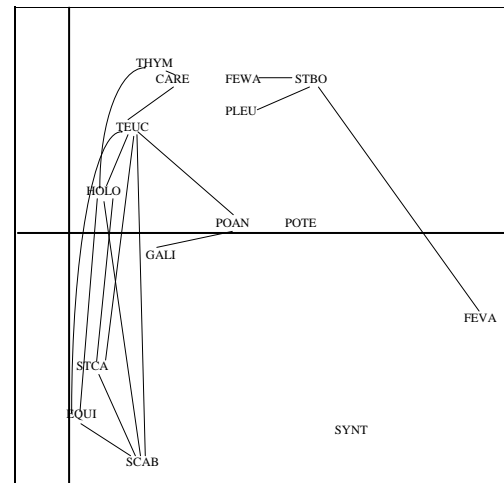


Fig. 8. Plexus graph of the species of Plot 5. (Details are given at Fig. 6).

In Plot 6 (shrubby habitat) the dominant coalition is built from eight closely connected species. The subordinated coalition consist of two grass species (POAN and FEVA), one herb (ASPE) and CARE which is one of the most frequent species in the study sites.

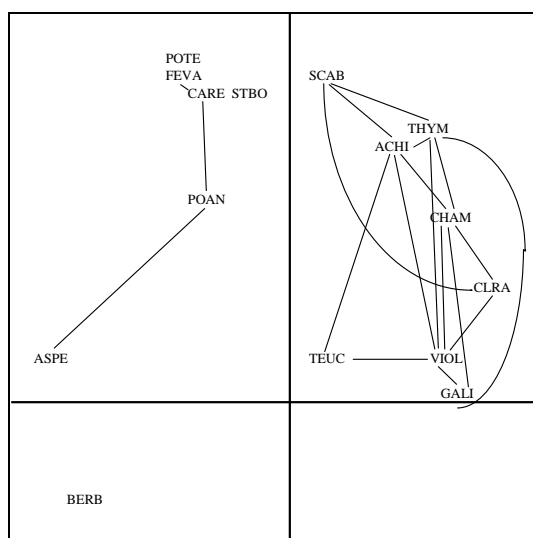


Fig. 9. Plexus graph of the species of Plot 6. (Details are given at Fig. 6).

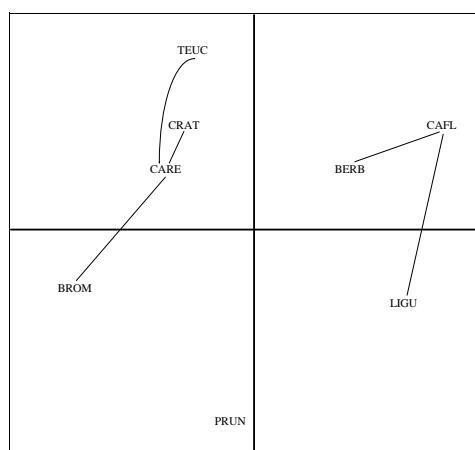


Fig. 10. Plexus graph of the species of Plot 7. (Details are given at Fig. 6).

In the understory vegetation of the poplar forest two small coalitions can be found, similar to the open grassland sites (Fig. 10).

Discussion

Species association and succession

The three distinguished association level category (Low, Medium and High) correspond with three successional steps. The same three category of these study sites were established using diversity ordering (Margóczy, 1993).

Leps and Buriánek (1990) found no consistent trend, Myster and Pickett (1992) described a decline in the changes of the frequency of significant

associations with the successional age of the old field. Bartha (1992) pointed out that using a careful scaling procedure and large samples higher number of species combination can be detected even in the case of relatively simple, undeveloped early successional plant assemblages. In present study the sample size is smaller than recommended by Bartha (1992), but the associatum values even at plot size 20x20 cm show differences of the studied vegetation types, and determine a possible successional order of them (Fig. 3). This is because our study sites represent different successional stages of a highly natural vegetation, and it is not an oldfield, studied by Leps and Buriánek (1990) and Myster and Pickett (1992), or not weed community, studied by Bartha.

Species association frequency and intensity as a measure of community organization degree

Departure from the random reference was very low in the above mentioned small spatial scale, but at larger scale (plot size 20x160 cm) it was considerable (Fig. 4). The higher the species number, the larger the difference between the real and random values (Fig. 5), indicating, that the detected increase of species association intensity and frequency is not a trivial statistical phenomenon, but refers to the organization degree of the studied communities. So only the sparse, pioneer vegetation of Plot 1 can be regard as randomly organized. The co-occurrence of plant populations is restricted by assembly rules (Wilson, 1991) in the other five study sites. Although we tried to choose spatially homogenous patches for the study, it cannot be excluded, that a certain degree of soil micro- heterogeneity influenced the spatial organization of the vegetation.

Spatial dependence of the detectability of species associations

Careful spatial scaling is recommended to reveal all of the relevant species combinations (Bartha, 1992; Szolláth and Bartha, 1991). In this work we found that the rank of the studied stands did not change considerably when regarding the maximal value at appropriate spatial scale and the value at 20x20 cm sampling unit size. The same was found both in the case of pairwise associations or associatum (Figs. 2 and 3). Only the Plots 4 and 7 has different character in this respect. The detectability of species associations is more spatial dependent here, than in the other five study plots. The association intensity is low at low spatial scale, but the maximal value is relatively high. Further analysis will be required to reveal the reason of this phenomenon. Presumable these study plots represent

not a single, intact community, but a complex of several transitional or disturbed patches.

Species coalition structure

In the plots of Low level association category (Plot 1 and 4) no coalitions were revealed on the basis of pairwise associations. Two coalitions were found in the other 5 study plots. In the plots of Medium level association category the species number of the coalitions was low and equal. The species number of the coalitions was 9 and 3 in the closed grassland (Plot 5), and it was 8 and 4 in the shrubby habitat (Plot 6). The latter species coalition structure is rather similar to that of found by Seffer and Stanova (1993) in an acidophilous sand dune, where 10 species formed a larger coalition and other three species a smaller one. The size of the coalitions revealed by plexus-graph method was very similar in the study of Matus and Tóthmérész (1990) as well: 10 and 3 in an undisturbed sand grassland, and 8 and 2 in the grazed part of it. These results suggests, that in sand grassland communities plant populations are grouped generally in two separate coalitions, one of it with higher species number, and the other with low species number. Present study does not provide any suggestion about the nature of the assembly rules forming such coalition structure. Population level approach is necessary to find them.

The coalitions in Plot 5 can be differentiated according to the drought tolerance character of the members. This is in good agreement with the result of Körmöczi and Balogh (1990) that drought tolerance is important driving force of the spatial distribution of species in different communities of sand vegetation.

Acknowledgments

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