

INTERSPECIFIC ASSOCIATIONS IN DIFFERENT SUCCESSIONAL STAGES OF *BRACHYPODIUM PINNATUM* GRASSLAND AFTER DEFORESTATION IN HUNGARY

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Abstract. At the border of the Hungarian Central Mountain Range and the Hungarian Great Plain *Brachypodium pinnatum* is a dominant component of the herb layer of *Quercus pubescens* oakwood. In Hungary, *Brachypodium* grasslands are of very high diversity and natural conservation value because they preserve many elements of the original forest-steppe flora. During the secondary succession after deforestation xeromesophilous *Brachypodium pinnatum* community develops and gradually turns into xerophilous grasslands.

Spatial organization and compositional differentiation of *Brachypodium pinnatum* communities were studied in three stands representing their early, middle, and late secondary successional phases. Presence/absence of species were detected in 20×110 grids of contiguous 5×5 cm micro-quadrats, and analysed by using information statistics.

Early phase was characterized by a coalition of mesic species. Xeric and mesic grasses formed coalition in the middle phase but they were segregated in the late successional phase. However, the pattern of species replacement was diffuse and gradual during the transformation process.

Keywords: information theory, spatial pattern, xeromesophilous grasslands, fine-scale spatial organization, species coalitions

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Introduction

Statistically determined associations between species and species groups are considered to be an important feature of a plant community (Kershaw and Looney 1985).

Analysing the spatial pattern of individual species in natural and disturbed communities has been still very frequent, and interest in this topic has been continued since the pioneering work of Greig-Smith (1952,1961), Hurlbert (1969) and Kershaw (1959, 1960, 1963). While in the „golden age” of pattern analysis about 20 years ago (Greig-Smith 1983, Kershaw 1973, 1985, Schluter 1984) at most one and two-species patterns were studied, recently multispecies patterns (e.g. Bartha 1992, Juhász-Nagy 1976, 1984, Podani *et al.* 1993, Dale 1991, 1995) and coalitions or functional groups have been received considerable attention (Wilson *et al.* 1994,

Bartha *et al.* 1995). Several authors emphasized the importance of frequency changes of significant interspecific associations in successions (O'Connor and Aarssen 1987, Leps and Buriánek 1990, Matus and Tóthmérész 1990, Myster and Pickett 1992 and Margóczy 1995). Van der Maarel stressed in one of his reviews (1996) the ecological significance of time sequence of observations and spatiotemporal pattern analyses.

Recently increasing evidences suggest that complex patterns of vegetation and species populations exist at a range of spatial and temporal scales. Great stochastic spatiotemporal variability in distribution and abundance of species or species groups was often revealed which was in many interpretations considered to be an inherent stochastic character of successional patterns to support the individualistic and stochastic concept of vegetation. However, there are many results even at fine-scales, which contradict

to the individualistic view and show deterministic feature of the relationships between species and populations (Gigon 1996) or non-randomness of pattern of individual species (Turkington *et al.* 1985, Thorhallsdóttir 1990, Watkin and Wilson 1992). Challenges for ecologists to know more about the spatial organization of species during successions have still remained.

In this paper we study the compositional differentiation of a xeromesophilous *Brachypodium pinnatum* community at fine-scale. Transformation of species composition, fine-scale spatial patterns and coalition structures were analysed along a successional gradient characterized by the gradual change of xeromesophilous *Brachypodium pinnatum* community into xerophilous ones.

This work is part of a larger project dealing with vegetation dynamics, as well as species replacement and microstructure changes of *Brachypodium* communities at different spatial and temporal scales.

The main purpose of the present paper is to reveal the differences in the fine-scale structure of local species coexistence in a changing vegetation of different successional stages. We are especially interested in the changes of pairwise associations between species.

Two hypotheses were tested. Whether 1) species replacements are diffuse and random or particular coalition structure is developing, as well as 2) xeric and mesic species are assembled randomly or they are segregated into microhabitats of different light conditions and water availability.

Material and methods

Study site

Field studies were carried out in a local nature conservation area in the north part of Hungary.

The investigated area is located 25 km east of Budapest at the border of the Gödöllő Hills. The area is part of a forest steppe zone at an altitude of 200-230 m above sea level. The climate of the area is intermediate in character between the continental climate of the Great Plain and the subcontinental climate of the hilly-country. The mean annual temperature is 9 °C and the mean annual precipitation is about 600 mm. Brown forest soil of chernozem character is typical on the loess substrate.

The study area was formerly covered by dry *Quercus pubescens* oakwood. Most of it was cut in the early 1900's (Military Survey 1883, 1943). This forest activity resulted in a wide range of habitats in which diverse vegetation types formed by local secondary successions of different directions and

rates. Nowadays, remnants of forest, shrub vegetation and a series of grassland communities of xeromesophilous to xerophilous character can be found along the 2 km long northeasterly slopes of the loess valley. For more details about the description of the vegetation and its landscape-level heterogeneity see Fekete *et al.* 1998.

Brachypodium pinnatum plays a central role in the course of secondary succession following deforestation. This species was the dominant component of the sparse undergrowth layer of the former dry oakforest.

The stands of *Brachypodium pinnatum* (forest remnants) have survived for many decades after deforestation. Some of them are able to preserve many shade-tolerant forest species, while the others become saturated by the xerothermic grassland species. Characteristically, the stands of *Brachypodium pinnatum* community of the open and sunny areas became closed and dense after the removal of trees. Gradual abundance decline of *Brachypodium pinnatum* through the secondary succession can be regarded as long term responses to the lack of forest microclimate and tree canopy closure.

Our target object is a xeromesophilous *Brachypodium pinnatum* community, which represents an intermediate stage along a forest - steppe floristic gradient on the study area. It has developed during the secondary succession after deforestation and it is gradually turning into xerophilous communities (Fekete *et al.* 1998).

Three types of the xeromesophilous *Brachypodium pinnatum* community developed during the past 100 years were selected for the present study. They are different floristically and coenologically from each other in various degree, however these „communities” did not receive a separate syntaxonomical status. For convenience, the terms of „community” and „stages” will be used alternatively further in this paper.

These communities are as follows:

Forest-type of *Brachypodium pinnatum* community represents an early phase of secondary succession. It can be found along the edge of *Crataegus monogyna* shrub on slopes influenced by shadow of *Crataegus* plants and also of small groups of white oaks. Coverage of *Brachypodium pinnatum* amounts to 60-70% or more. The stand is dense and closed, where the average height of the sward is about 50-60 cm. A litter thickness is 10-15 cm. It preserves numerous shade-tolerant forest plant species as rests of the earlier forest, whereas the number of steppe plants is very low here.

Transitional-type of *Brachypodium pinnatum* community representing the middle successional

phase is a so-called mixed type of high mesic and xeric species diversity dominated by many dicots and broad-leaved grasses. The sward is of low saturation, with light closure (50-60%). The height of sward is 30-45 cm, the litter thickness is 5-10 cm. Total cover of *Brachypodium pinnatum* is only 15-35%. Many xeric species are favoured by *Brachypodium* canopy thinning. Coverage of *Festuca rupicola* — pioneer of xerothermic grasslands — often also amounts near 25%. The number of steppe species is relatively high approaching to 15-20, and their total cover is sometimes considerable (35-55%).

Steppe-type of *Brachypodium pinnatum* community represents a late successional stage of the gradient from forest to steppe. The height of sward is 30-35 cm, and the litter thickness is only 2-6 cm. It mainly develops on upper part of slopes to S, so its habitat is fairly warm and dry. The forest plants tolerant to shade are strongly suppressed here. Coverage of *Brachypodium pinnatum* considerably decreased and the vitality of this grass is much lower than it was in the former vegetation type, yellowing of leaves can often be observed. Gaps in the sward are significant giving opportunity for colonizing more and more steppe plants. Abundance of *Festuca rupicola* and many other steppe plants is considerable.

Field sampling

We chose physiognomically uniform stands of each community occurring close together in space. They are all surrounded by *Bromus erectus* grasslands, which means a similar coenological environment in the neighbourhood of each stand. The stands of three successional stages represent also a light gradient associated with the declining dominance of *Brachypodium pinnatum*.

At a fine-scale 25 cm² contiguous plots were sampled. Presence/absence of species were detected in 20×110 grids of contiguous 5×5 cm microquadrats in June. Vegetative units of all plants rooted in microplots were also counted. For all graminoids vegetative units are defined as tillers. Small seedlings with only young small leaves were not included, since they differ much from the more established plants, as well as from their dynamics (Herben *et al.* 93).

Computerized sampling and data analysis

From the 20×110 grids of presence/absence data computerized sampling were performed (Podani 1984a,b, 1992). Repeating the sampling procedure with increasing sampling unit sizes across a range of

scales between 5×5 cm and 5×150 cm, we created a series of 2×2 contingency tables for each pair at each scale. Association between two species was computed from the 2×2 contingency table and it was expressed by their mutual information, $I(A,B)$ (see Juhász-Nagy 1980, 1984, and Juhász-Nagy and Podani 1983 for details of the computation.) Significant associations were detected by Monte Carlo randomization tests. We applied complete randomization (Diggle, 1983) that randomizes completely the positions of individuals (the presences in our case) of each species within the whole grid (Site model, Watkins and Wilson 1992), but keeps the number of species and their frequencies constant, i.e. same as in the field. Significance of observed value can be calculated as probability of the observed value under the null hypothesis, i.e. the proportion of Monte-Carlo randomizations in which the random $I(A,B)$ is more extreme than the observed value. 5000 randomizations were applied in each test. The sign of associations was detected by comparing the sums of the frequency of the diagonal cells in the 2×2 contingency table (comparing a+d to b+c) (Kershaw 1964). According to our experiences (Bartha and Kertész unpublished), beside the interspecific spatial dependence, this method might detect additional significant positive associations due to autocorrelations (i.e. the aggregated patterns of species) as well. When we repeat the analyses at several sampling unit sizes, the interval of spatial scale of significant associations increases due to autocorrelations. Textural constraints also influence these scales (Bartha and Horváth 1987, Tóthmérész and Erdei 1992). The type of randomization applicable to grids does not allow us to separate these effects. Therefore, we did not interpret the scale of associations. After surveying the significant associations at all sampling unit sizes, an association was considered to be positive if it was always positive. If the sign of associations between two species changed with scale, we considered it as negative, because the additional positive association might indicate autocorrelation only. The same technique was successfully applied for successional data by Bartha (1992). Frequency of significant positive and negative associations were calculated for each successional stage (expressed as percentage of the potential maximum, i.e. the number of possible species pairs). To avoid artefacts due to rarity and due to the limited sample size, rare species (with frequency less than 1%) were omitted from the analyses.

Plexus diagrams depicting the significant positive and negative associations (McIntosh 1978) were displayed in the case of all species and only for the graminoids.

Considering the coenological and ecological affinities of the species we distinguished 3 groups of species (guilds) in our site, such as the so-called forest species (i.e. mostly mesic, shade-tolerant species), the steppe species (i.e. mostly drought-tolerant and light-demanding xeric species), as well as the „indifferent” species. Thus, the significant associations were also evaluated with respect to these 3 species groups, from which changes in the first 2 groups are likely responsible for the outcome of secondary succession.

Results

Textural attributes

All stands are dominated by vegetatively spreading perennial species. Altogether 60 species were detected in the 3 stands. Some textural attributes in 3 stages of succession are presented in Tables 1 and 2.

It is remarkable, that the proportion of rare species (freq.:<1%) is very high accounting for 68, 57 and 58% of the total number species of each of the stands. In general, very few dominant and codominant (freq.:>5%) species (7,8 and 11) occur in all stands. Most of the species appear in the middle successional stage, but many codominant (50%) species are apperant in the steppe-like *Brachypodium* stand (=late successional stage). *Brachypodium pinnatum* appears to be fairly ubiquitous in the forest-like stand (early stage of succession), where its predominance can result the lowest species richness.

The secondary succession can be characterized by the decreasing dominance of *Brachypodium pinnatum*. Its pathway is thought to be affected by the changes in species abundance, pattern of individuals and varying light conditions. A clear trend of decreasing abundance of mesic and increasing abundance of xeric perennial species along the successional gradient is well-expressed (Table 1), such as the changes of the number of light-demanding xeric species from 25% to 54%. As Table 1 shows, there is only a slight decrease in the frequency of *Brachypodium* along the mesic to xeric successional gradient measured in the microquadrats. However, the considerable decrease of its cover, the decreasing height of tillers, and the lower litter thickness found in the Transitional and Steppe-type indicate indirectly the decreasing viability of *Brachypodium* clones exposed to light and drought after deforestation. Note that the abundance differences are much more considerable also in the

case of *Festuca rupicola* and *Bromus erectus*, than their frequency values.

Table 1. Some textural attributes in 3 successional stages of *Brachypodium pinnatum* grassland after deforestation in Hungary

| | Forest-type | Transitional-type | Steppe-type |
|------------------------------------|-------------|-------------------|-------------|
| total cover | 100 | 130 | 115 |
| litter thickness | 10-15 cm | 5-10 cm | 2-6 cm |
| average height of the sward | 50-60 cm | 30-45 cm | 30-35 cm |
| total species richness | 50 | 60 | 53 |
| number of frequent species | | | |
| frequency % ≥ 1 | 16 | 26 | 21 |
| frequency % ≥ 5 | 7 | 8 | 11 |
| frequency % ≥ 10 | 3 | 5 | 6 |
| mesic species (% of total species) | 62 | 52 | 42 |
| xeric species (% of total species) | 25 | 46 | 54 |
| cover % | | | |
| <i>Brachypodium pinnatum</i> | 74.9 | 35 | 22 |
| <i>Festuca rupicola</i> | 3.6 | 7.7 | 15.4 |
| <i>Bromus erectus</i> | 23 | 17.6 | 20 |
| frequency % | | | |
| <i>Brachypodium pinnatum</i> | 79 | 63 | 52 |
| <i>Festuca rupicola</i> | 23 | 17.6 | 20 |
| <i>Bromus erectus</i> | 5.5 | 24.7 | 25 |

An approximation of the coalition structure with plexus graphs

In the Forest-type community there are only positive associations (27 in total) between the species. The graph is of reticulate character, majority of species is mesic (Fig. 1a,b, Table 3). The mesic grasses (e.g. *Dactylis glomerata*) and dicots (e.g. *Betonica officinalis*) with low frequency appearing in the small openings of the stand are infiltrated (intermingled with) between the more frequent species. No expressed multi-coalition structure is apparent.

The largest number of significant positive (27) and negative (32) associations were detected in the middle successional stage (Fig. 2a,b). Many mesic and xeric species are mixed with each other forming significant associations. Dicots except of tall species with very deep, weel-developed root system (e.g. *Achillea pannonica* - *Helianthemum ovatum*,

Table 2. Abundance hierarchy of the species in 3 successional stages of *Brachypodium pinnatum* grassland after deforestation in Hungary (Percentage frequency of species (>1 %) in the 20 × 100 grids is presented)

| Forest-type | | Transitional-type | | Steppe-type | |
|-----------------|-------------|-------------------|-------------|-----------------|-------------|
| Code of species | Frequency % | Code of species | Frequency % | Code of species | Frequency % |
| BRAPIN | 79.5 | BRAPIN | 63.1 | BRAPIN | 52.4 |
| FESRUP | 23.7 | BROERE | 24.7 | BROERE | 25.8 |
| TEUCHA | 11.2 | CARHUM | 18.5 | FESRUP | 20.3 |
| CARCAR | 7.4 | FESRUP | 17.6 | CARCAR | 12.6 |
| POAANG | 6.4 | CARCAR | 13.9 | FILVUL | 11.6 |
| BROERE | 5.9 | HELOVA | 9.6 | THYPAN | 10.5 |
| ARRELA | 5.5 | ARRELA | 7.6 | CARHUM | 9.2 |
| FILVUL | 4.5 | SESANN | 6.7 | SESANN | 8.6 |
| FALVUL | 4 | ACHPAN | 4.8 | TEUCHA | 8.4 |
| SESANN | 3.6 | TRIMON | 4.1 | TRIMON | 5.7 |
| THYPAN | 3.5 | EUPPAN | 4 | PHLPHL | 5.3 |
| TRIMON | 3.3 | DACGLO | 3.3 | BOTISC | 3.6 |
| PHLPHL | 2.4 | TEUCHA | 3.2 | MEDFAL | 3.1 |
| GALVER | 2.2 | CAMRIT | 3.1 | AGRREP | 2.5 |
| DACGLO | 1.2 | PIMSAX | 3 | KOECRI | 2.4 |
| BETOFF | 1 | MEDFAL | 2.9 | THLJAN | 1.7 |
| | | KOECRI | 2.8 | CHRGY | 1.6 |
| | | FILVUL | 2.8 | DACGLO | 1.5 |
| | | CHAAUS | 2.7 | CAMROT | 1.2 |
| | | ASTONO | 1.7 | ARRELA | 1 |
| | | VIORUP | 1.6 | HELOVA | 1 |
| | | PHLPHL | 1.5 | | |
| | | SILVUL | 1.1 | | |
| | | CENSAD | 1 | | |
| | | AGRREP | 1 | | |
| | | BRIMED | 1 | | |

Table 3. List of species indicated in the plexus graphs

| Name of species | Code | Guilds | Name of species | Code | Guilds |
|---------------------------------|---------|-------------|-----------------------------|--------|-------------|
| <i>Achillea pannonica</i> | ACHPAN | xeric | <i>Festuca rupicola</i> | FESRUP | xeric |
| <i>Agropyron repens</i> | AGRREP | xeric | <i>Filipendula vulgaris</i> | FILVUL | mesic |
| <i>Arrhenatherum elatius</i> | ARRELA | mesic | <i>Galium verum</i> | GALVER | mesic |
| <i>Astragalus onobrychis</i> | ASTONO | xeric | <i>Helianthemum ovatum</i> | HELOVA | xeric |
| <i>Betonica officinalis</i> | BETOFF | mesic | <i>Koeleria cristata</i> | KOECRI | xeric |
| <i>Bothriochloa ischaemum</i> | BOTISC | xeric | <i>Medicago falcata</i> | MEDFAL | xeric |
| <i>Brachypodium pinnatum</i> | BRAPIN | mesic | <i>Phleum phleoides</i> | PHLPHL | xeric |
| <i>Briza media</i> | BRIMED | indifferent | <i>Pimpinella saxifraga</i> | PIMSAX | indifferent |
| <i>Bromus erectus</i> | BROERE | mesic | <i>Poa angustifolia</i> | POAANG | mesic |
| <i>Carex caryophylla</i> | CARCAR | indifferent | <i>Seseli annuum</i> | SESANN | indifferent |
| <i>Carex humilis</i> | CARHUM | xeric | <i>Silene vulgaris</i> | SILVUL | indifferent |
| <i>Centaurea sadlerana</i> | CENTSAD | indifferent | <i>Teuchrium chamaedrys</i> | TEUCHA | mesic |
| <i>Chamaecytisus austriacus</i> | CHAAUS | xeric | <i>Thlaspi jankae</i> | THLJAN | xeric |
| <i>Chrysopogon gryllus</i> | CHRGY | xeric | <i>Thymus pannonicus</i> | THYPAN | xeric |
| <i>Dactylis glomerata</i> | DACGLO | mesic | <i>Trifolium montanum</i> | TRIMON | indifferent |
| <i>Euphorbia pannonica</i> | EUPPAN | xeric | <i>Viola rupestris</i> | VIORUP | xeric |
| <i>Falcaria vulgaris</i> | FALVUL | indifferent | | | |

Astragalus onobrychis - *Chamaecytisus austriacus*) are usually positively associated, whereas between graminoids and between graminoids and dicots both positive and negative associations prevail. A lot of relatively rare species with low frequency also play a role in developing the complicate association structure of this type. We stress here the importance

of positive associations of some xeric graminoids, such as *Festuca rupicola*, *Carex humilis*, *Koeleria cristata* with other graminoids and dicots, as well.

In the Steppe-type *Brachypodium* stand a complex association structure among the species is also peculiar, similarly to the former community (Fig. 3a). The number of positive and negative

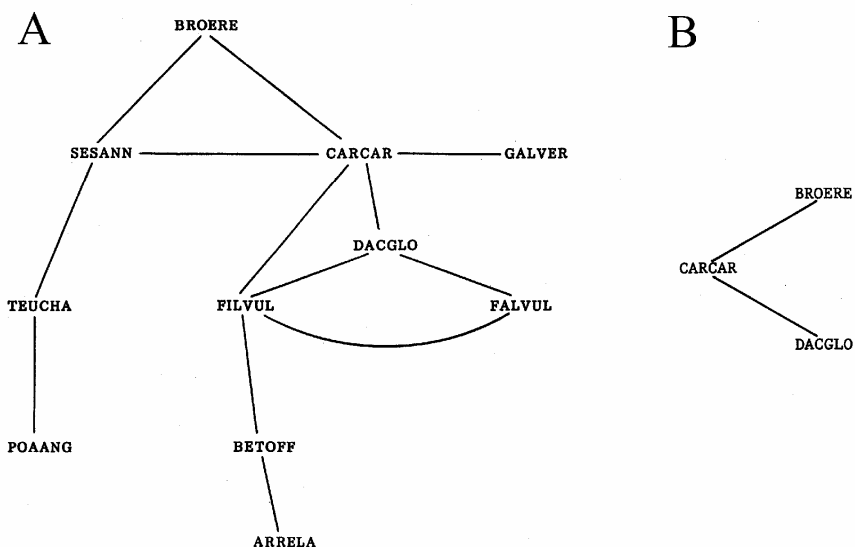


Fig. 1. Plexus diagram for species of an early successional *Brachypodium* coenostate (significant pairwise associations ($p < 0.01$): — positive, ---- negative, A: between monocots and dicots, B: between monocots). (Abbreviations are in Table 3.)

associations is near the same, but both are less, than in the middle stage (17 +, 18 -). It is important that between the perennial graminoids only negative associations appear with one exception (Fig. 3b). It is very likely that the growth habit of grasses partly accounts for the negative values. In this late successional stage mostly xeric species form coalitions and strong spatial segregation of graminoids is characteristic. The community may be divided into 2 coalitions. *Bothriochloa ischaemum*, *Seseli annuum*, *Helianthemum ovatum*, *Thlaspi jankae*, *Trifolium montanum* are positively associated in the first coalition, while positive associations appear between *Phleum phleoides*, *Chrysopogon gryllus*, *Teuchrium chamaedrys* and *Filipendula vulgaris* in the other coalition. These coalitions were separated from each other by many negative associations.

If we consider the significant associations between the 3 groups of species („guilds”) differentiated by their ecological requirements (Table 3), much higher number of significant positive and mainly significant negative associations can be found between guilds than within guilds in each community. The greatest differences are in the case of the final stage of secondary succession.

| | % number of significant associations | |
|-------------------|--|--|
| | within guilds (% of within-guild total) | between guilds (% of between-guild total) |
| Forest-type | 8.5 (8.5 +, 0 -) | 17.8 (16.4 +, 1.4 -) |
| Transitional-type | 11.8 (6.3 +, 5.5 -) | 15.9 (8.2 +, 7.7 -) |

| | | |
|-------------|--------------------|---------------------|
| Steppe-type | 7.4 (4.3 +, 3.1 -) | 14.7 (6.6 +, 8.1 -) |
|-------------|--------------------|---------------------|

Discussion

Trends of species associations in succession

A decreasing trend of the frequency of significant associations (standardized by the number of possible species pairs) has been found during the secondary succession. The frequency % changing from 14.2, 12.9 to 10.2% corresponded with the 3 successional stages studied. Our result is in good agreement with the general experience that a declining tendency in the changes of the frequency of significant associations with the successional ages is rather typical (Myser and Pickett 1992). However, no consistent trend in old fields was also pronounced (e.g. Leps and Burjáněk 1990).

Coalition structure

In our communities expressed differentiation into well-separated species coalitions could not be found in contrast with the results obtained by Margóczy (1995) and Matus and Tóthmérész (1990) in their natural and grazed sandy communities. Highly complex association structures were revealed in the successional stages of a transforming process of the xeromesophilous *Brachypodium* community. Our grassland types are well-structured with complex multispecies coalitions as compared to the sandy

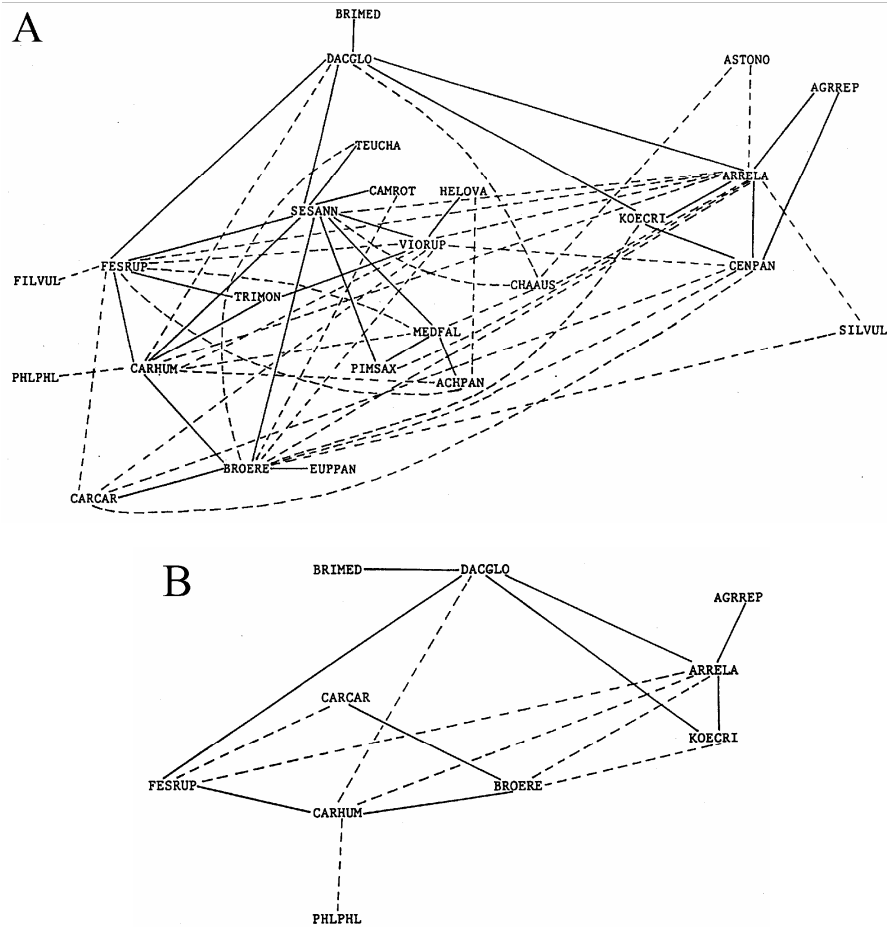


Fig. 2. Plexus diagram for species of a middle successional *Brachypodium* coenostate. (Explanation for symbols see in Fig. 1 and Table 3.)

grasslands with relatively simple coalitions of few species.

Most characteristic feature of forming species associations in 3 successional stages of a transforming vegetation

In our communities the number of significant associations was relatively low (10-14%) suggesting diffuse competition between species (Leps and Burianek 1990). Great differences were revealed how the individual species were spatially assemblaged in the 3 successional stages. The Forest-type community including only positively associated species (mostly mesic ones) was separated from the 2 later successional stages. The most complicated reticulate plexus graph with the highest number of the significant positive and negative associations were detected in the middle phase of succession.

Strong segregation of graminoids and development of well-structured coalitions were initiated in the late successional phase.

Plexus graphs analysed varied considerably between successional stages. Early phase was characterized by a coalition of mesic species. Xeric and mesic grasses formed a coalition in the middle phase but the graminoids were strongly segregated spatially in the late successional phase.

We conclude that between communities on a local scale a slow shift of dominance hierarchy took place and habitat selection had also acted. Particular local coexistence structure was typical referring to the different communities. Some exclusion of species combinations was also going on mainly caused by textural and microtopographical constraints. We suggest that the decrease of the dominance and abundance of *Brachypodium pinnatum* modified the micro-environmental conditions (light intensity

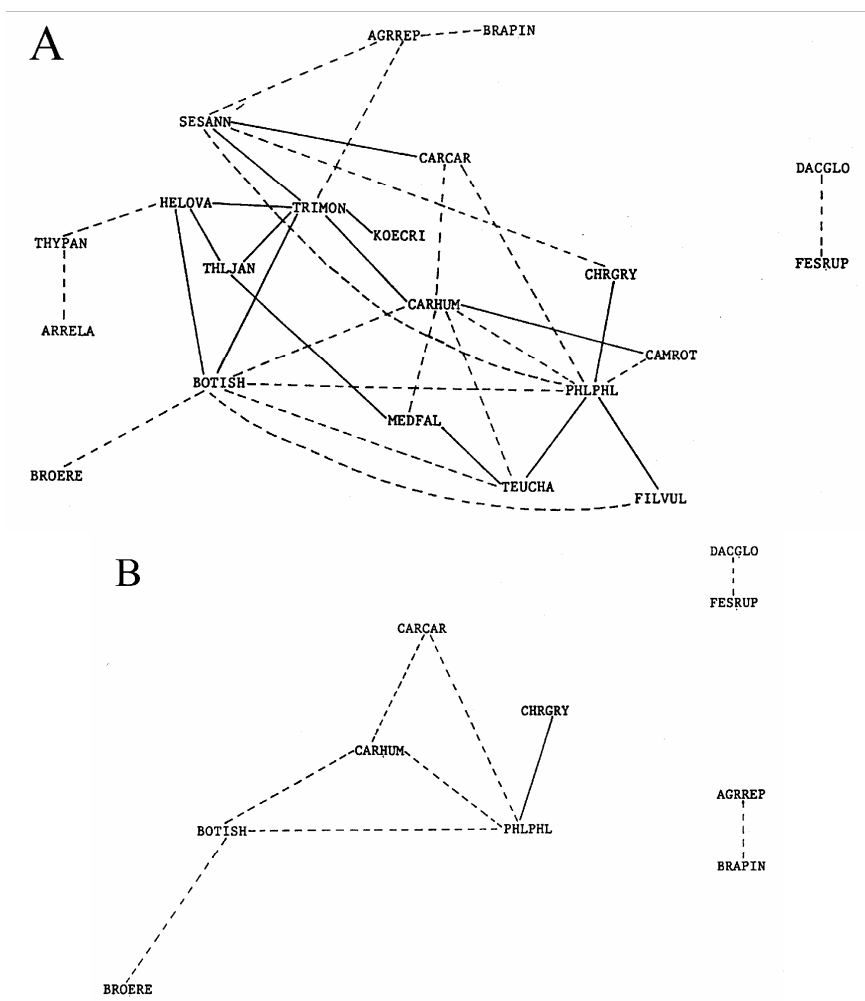


Fig. 3. Plexus diagram for species of a late successional *Brachypodium* coenostate. (Explanation for symbols see in Fig. 1 and Table 3.)

within a stand, degree of local colonization). Microheterogeneity of the stands influenced forming the species assemblages, as the species or species groups differently preferred the varying microsites and biotic and abiotic conditions in a dense or slightly dense stands of successional stages. The density of individuals, morphology, growth form, limited dispersal and spatial distribution of perennial plants were the most influential factors controlling the coexistence of species.

Thus, answering our first hypothesis, we can conclude that various coalitions are developing in succession. However, it is very likely that pattern of species replacement during the secondary succession is diffuse and gradual instead of a complete replacement of species at stand scale. It was

apparent that the species rather showed overlap and continuous transition among the successional stages.

As to the second hypothesis, we can state that in each successional stage most of the species showed non-random fine-scale spatial distribution. Aggregated spatial distribution of many species reflected different spatial microheterogeneity within each stand at fine scale. Forest and steppe species were not completely randomly assembled even at fine spatial scale. We stress that all our communities (states) dominated by perennial species spreading vegetatively were closed of high species saturation, where colonization by seeds were less significant. Fine-scale spatial heterogeneity was mainly caused by growth form of individuals. Dispersal was limited considering that the seeds could reach mainly adjoining microsite of the nurse plants and most

propagula were not able to grow in every microhabitat. As a consequence of these phenomena an individual stand was a mosaic of species populations showing particular spatial patterns. Matrix perennial graminoids played an important role in spatial organization. Their segregation in space was obvious. This feature was also found by Thorhallsdóttir (1990) in her community.

Thus, our findings seem to support the non-randomness of species assemblages, similarly with the results obtained by Gigon (1996), Hara (1993), Thorhallsdóttir (1990) and Watkin and Wilson (1992) in their communities. Our results are, however, partly in contradiction with van der Maarel's carousel model (Van der Maarel and Sykes 1993, 1997, Sykes *et al.* 1994) which assumes that each species can reach and survive each microsite in a community, i.e. the spatio-temporal turnover of species is random. Note that the alvar limestone grassland community studied by van der Maarel was homogeneous, grazed for a very long time and composed by mostly shortlived species. Carousel model might be valid for this species saturated, near the equilibrium community. However, species turnover seems to be well-structured in our spatially heterogeneous transitional communities. We suggest that interspecific spatial associations are dependent on a patchy microenvironment induced by the variation of local population densities, dispersal limitations and limited plant propagations.

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