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Interspecific associations in old-field succession

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Abstract. Interspecific associations were determined on the basis of quantitative (cover) and qualitative data in three old-fields of different age and in nearby natural forest in the Bohemian Karst, Czechoslovakia. No consistent trend was found in changes of the frequency of significant associations with the successional age of the field. The pattern of species associations was analysed with respect to phenological similarity of species and with respect to life histories of species. The hypothesis that phenologically similar species compete more than phenologically dissimilar species and consequently are spatially segregated is only weakly supported by the data from the oldest field. Except in the youngest field, differences were found between associations of species belonging to various groups. The associations among annuals were mostly positive; the strongest negative associations were found among perennial grasses. The frequency of significant associations may be regarded neither as a measure of biological organisation, nor as a measure of the competition strength.

Introduction

Statistically determined associations between species are considered to be an important characteristic of a plant community (Kershaw and Looney 1985). Changes in the pattern of interspecific associations in the course of succession or in variously disturbed communities have been investigated (e.g. Greig-Smith 1952, Kellman 1969, O'Connor and Aarssen 1987). In early interpretations, the frequency of statistically significant associations was considered to reflect the degree of biological organization of a community, and its decrease in 'stable' or late successional communities was considered to support the individualistic concept of plant communities (Kershaw 1973). In a recent paper (O'Connor and Aarssen 1987), the pattern of associations is related to the competitive structure.

The aim of this paper is to answer following questions:

1. Are there any changes in the pattern of interspecific associations in the course of secondary succession?

2. Are there any relationships between ecological and/or morphological similarity of species and their spatial relationships?

Within the second question, two hypotheses were tested.

(a) Species with similar phenology are supposed to compete more than species with differing phenology and as a consequence they should be spatially segregated. A negative correlation is expected between a measure of phenological similarity and a measure of interspecific association. This assumption was proposed by Hurlbert (1969).

(b) Strong competitors are supposed to be spatially segregated (to be negatively associated); weak competitors are supposed to be found together in the "gaps" between the strong competitors and are expected to be positively associated.

Material

The structure of vegetation in three old-fields differing in age and in natural forest nearby was investigated in the framework of a larger project on old-field succession in the Bohemian Karst (Osbornová *et al.* 1990). The Bohemian Karst is a limestone area in Central Bohemia, Czechoslovakia. The climate is summer-warm and dry (annual averages 8°C and 370 mm of precipitation). The natural vegetation in the area consists of thermophilous forests dominated by *Quercus petraea*, *Q. pubescens* and *Carpinus betulus*, and species-rich rocky steppes, particularly on south-facing limestone slopes.

Two successional seres were distinguished in old-field succession — the xeric one and the mesic one. The investigated fields belong to the xeric sere (intensively studied fields labelled X1, X2 and X3 in Osbornová *et al.* 1990). All three fields are situated in the same position on the tertiary Berounka river terrace (mainly acidic sediments on limestone parent rock) near the village of Srbsko. The youngest field (size 15 × 50 m) was sampled in the first four years after abandonment (1979 to 1982). The last crop was wheat, the field was ploughed after harvesting. The medium aged field (15 × 60 m) was sampled at the age 7 and 11 yrs (1976,1980) and the oldest field (40 × 30 m) at the age of ca. 55 yr (1975). For comparison, some investigations were carried out in the ground layer of a forest of a natural species composition on limestone approx. 4 km away from the investigated old-fields.

In the first year, the old-field vegetation consisted mainly of annual weeds. The most abundant was *Papaver rhoeas*, other species were *Fagopyrum convolvulus*, *Medicago lupulina*, *Galium aparine* and *Veronica* spp. In subsequent years, annuals were subsequently replaced by biennials and perennials (mainly *Artemisia vulgaris*, *Agropyron repens*, and *Daucus carota*, *Taraxacum officinale*, *Achillea millefolium*). *Artemisia* and *Agropyron* were abundant in the 4-th year of the youngest field and were dominant in the medium aged field about its 7-th year. Then they lost ground to other species, mainly perennial grasses. The oldest stadium was without any directional change in the last years (1975 to 1988). It was dominated by narrow-leaved perennial grasses *Festuca rupicola* and *Poa angustifolia*. The forest ground layer was without any apparent dominant. It was species rich with mainly broad-leaved perennials, for example *Lathyrus vernus*, *Sanicula europaea* and *Asarum europaeum*.

Within the larger project, manipulative perturbation experiments were carried out in the medium-aged and the old plots. In particular, increase of biomass of unaffected

species after application of selective herbicides (Michálek, Buriánek and Hadincová 1990) has demonstrated influence of competition. This enabled comparison of evidence obtained from manipulative experiments and from analysis of distributional patterns.

Methods

The interspecific associations at the 1 m^2 scale were determined in the first four years of the youngest field, at age 7 yrs of the medium aged field, in the oldest field and in the forest ground layer once (in 1975). In each plot at each sampling date, forty 1 m^2 quadrats were analysed by the point quadrat method (Goodall 1952), 100 pins in a square grid in each quadrat. In this way, estimates of cover of all species were obtained. For the youngest field, the data are part of those used by Lepš (1987). The interspecific associations were determined on the basis of correlation coefficient r for all pairs of species with frequency higher than 10%. The frequency of statistically significant associations was determined (as a ratio of number of significant associations and number of all possible pairs of species with frequency higher than 10%) for all associations at $P < 0.05$, $P < 0.01$ and for positive associations at $P < 0.05$. Based on the same data, the heterogeneity of each plot (β-diversity) was determined as the difference between the diversity of pooled sample of all quadrats from the plot (γ-diversity) and average diversity in the quadrat (α-diversity). The diversity index H was computed according to the Shannon formula (logarithm base 2).

The interspecific associations on a small scale were determined once in each field (younger one at age 2 yrs, medium at 11 yrs, the oldest one at approx. 60 yrs). In each field, 150 squares 0.1 × 0.1 m were laid down and the root presence was noted in each. The interspecific associations were determined by usual analysis of 2 × 2 tables for all pairs of species. Species which appeared in 5 and fewer quadrats were excluded from the analysis. The significance of the association was tested by a χ^2-test and the strength of the association was expressed by the V coefficient:

$$V = \frac{(ad - bc)}{\sqrt{mnrs}} \tag{1}$$

where a, b, c and d are values of fields of 2 × 2 table and m, n, r and s are corresponding marginal totals.

On the medium aged and on the old-fields, the phenology of particular species was followed. At approximately two week intervals, the phenological phase of each species was determined. For computing the phenological similarity, only the data on flowering were used. The flowering in time t, $F(t)$ was assigned to equal 2 when most of the population was in flower, 1 if part of the population was in flower and 0 if there was no flowering. The phenological similarity of species i and j, $PS_{i,j}$ was then defined

$$PS_{i,j} = \frac{2\sum_{t=1}^{n} \min(F_i(t), F_j(t))}{\sum_{t=1}^{n} F_i(t) + \sum_{t=1}^{n} F_j(t)} \tag{2}$$

n is total number of time intervals sampled. The relationship between the association of two species V and their phenological similarity PS was evaluated by the correlation coefficient r. If there is a spatial exclusion of phenologically similar species, r is expected to

be significantly lower than zero. However, corresponding degrees of freedom (to estimate the variance of r and to test the null hypothesis: $r \geq 0$) are difficult to determine - particular values of coefficients are *not* independent variables. Consequently, the significance of the departure was tested using Monte Carlo permutation test. One of the matrices was subjected to random permutation of species and the correlation coefficient was computed. The significance was estimated from the proportion of values of r smaller than the original value of r. In most cases, 500 random permutations were used. The relationship is expected to be more pronounced in species competing with each other. Consequently, the same procedure was carried out with species pairs exhibiting the negative association only.

Species were divided into four (groups of) life forms: annuals, biennials, perennial grasses, perennial forbs. (No perennial grasses with sufficient frequency in the youngest field and no biennials in the oldest field were found). The average value of the coefficient V was computed for each combination of species life forms (i.e. annual - annual, annual - biennial, annual - perennial grass, etc.). The number of species pairs within a group is $\binom{n}{2}$, i.e. $\frac{(n-1)n}{2}$, between groups $n_1.n_2$ (n is number of species in respective group). For the same reasons as above, the Monte-Carlo permutation test was used to test the hypothesis that the value of the coefficient does not depend on the combination of life forms. (The appropriate number of life forms was randomly assigned to species). Two different test-criteria were used: the F-value for one-way ANOVA and absolute value of difference between the highest and the lowest group average. 500 random permutations were used.

Results

On the 1 m^2 scale, there is no consistent trend in the number of significant interspecific associations in the course of succession (Fig. 1). The percentage of significant associations is low (close to the number of associations resu ing from Type I error). Similarly, no consistent trend was found in the β-diversity (horizontal heterogeneity) of the plot. The forest ground layer has the lowest percentage of significant associations and very low β-diversity. Moreover, the structure of associations is difficult to interpret. As an example, the structure of interspecific associations in the medium aged and in the oldest fields are presented in Figs 2. and 3.

Similarly, neither consistent trend, nor striking differences in the number of significant associations determined on the basis of presence-absence were found (Table 1). In no case significant correlation was found between the strength of association and phenological similarity (Table 2). In the medium-aged field, the correlation was positive but very close to zero. In the old-field, the correlation was negative, as expected, but not significant. When only pairs exhibiting negative association were considered, the correlation was suggestive ($P = 0.065$). It suggests that in the older field the horizontal structure of the community might be shaped by competition more than in the younger one, or that in the older field there are some species pairs that are able to avoid competition by phenological differentiation. However, the evidence is weak.

The differences between average values of V in groups of species pair types are significant in the medium-aged and old fields and non-significant in the young field (Tables 3, 4, 5). In both cases where significant differences were detected, the average association

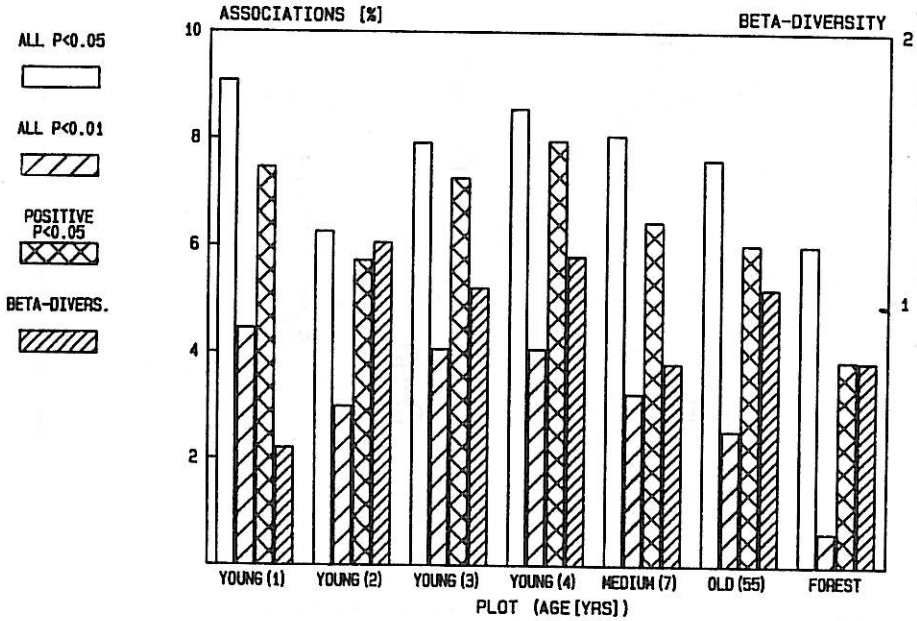

Fig. 1. Percentage of significant associations determined by correlation coefficients and β-diversity in old-fields of various ages and in the forest.

Table 1. Numbers of species included in the analysis and the percentage of significant associations detected by the χ^2 analysis of 2x2 tables.

field	number of species	percentage of significant associations for $P < 0.05$	for $P < 0.01$
young	26	3.08	1.23
medium aged	24	6.16	2.17
old	23	5.50	1.58

between pairs of annuals is positive and the average association between pairs of perennials is negative. The annuals are found together in gaps between the warp of perennial species. The averages are low in absolute values - however, note that for 150 sampling units $|V| > 0.16$ means significant association. The maximum possible value of V is determined by marginal totals (i.e. by frequencies of the species) and is low for a non-symmetrical table. Again, it seems that the differentiation of species competitive abilities increases with increasing field age. In the young field (age at sampling 2 yrs), the warp of perennial species was not present and the majority of species were annuals.

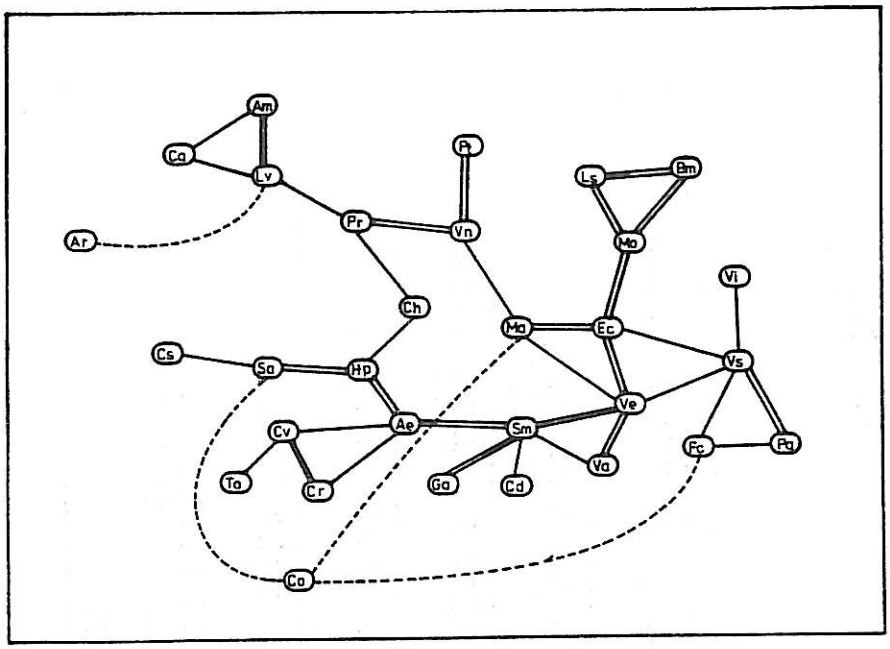

Fig. 2. The structure of interspecific associations determined by the correlation coefficients in the medium aged field. Straight full lines correspond to positive associations ($0.01 < P < 0.05$), double straight lines to positive associations ($P < 0.01$) and broken curves to negative associations ($P < 0.05$). Meaning of abbreviations: Ae – *Aegopodium podagraria*, Am – *Achillea millefolium*, Ar – *Agropyron repens*, Bm – *Bromus mollis*, Ca – *Cirsium arvense*, Cd – *Carduus acanthoides*, Ch – *Chenopodium album*, Co – *Convolvulus arvensis*, Cr – *Consolida regalis*, Cs – *Centaurea scabiosa*, Cv – *Coronilla varia*, Ec – *Eryngium campestre*, Fc – *Fallopia convolvulus*, Ga – *Galium aparine*, Hp – *Hypericum perforatum*, Ls – *Lactuca serriola*, Lv – *Linaria vulgaris*, Ma – *Myosotis arvensis*, Mo – *Melilotus officinalis*, Pa – *Poa angustifolia*, Pr – *Papaver rhoeas*, Pt – *Potentilla argentea*, Sa – *Silene alba*, Sm – *Stellaria media*, To – *Taraxacum officinale*, Va – *Viola arvensis*, Ve – *Veronica arvensis*, Vi – *Vicia angustifolia*, Vn – *Verbascum nigrum*, Vs – *Veronica sublobata*.

Table 2. Values of correlation coefficients r between the V-values and phenological similarity for all V values and for negative V values only and corresponding significances P (test of the null hypothesis $r \geq 0$).

	All V-values		Negative V-values	
	r	P	r	P
medium aged field	0.038	0.740	0.102	0.880
the oldest field	-0.047	0.255	-0.122	0.068

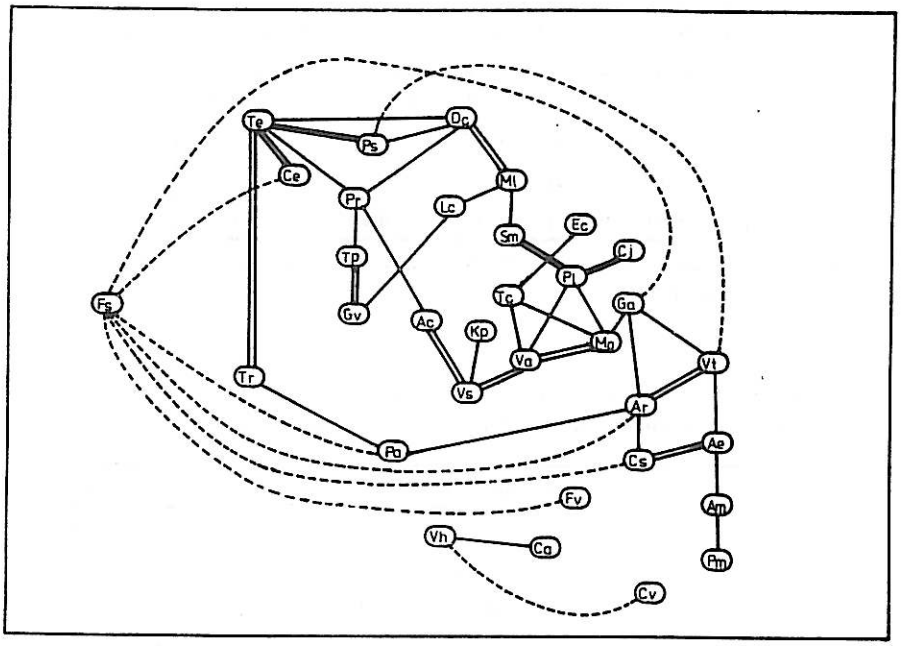

Fig. 3 The structure of interspecific associations determined by the correlation coefficients in the oldest field. Straight full lines correspond to positive associations ($0.01 < P < 0.05$), double straight lines to positive associations ($P < 0.01$) and broken curves to negative associations ($P < 0.05$). Meaning of abbreviations: Ac – *Asperula cynanchica*, Am – *Achillea millefolium*, Ar – *Agropyron repens*, Ae – *Arrhenatherum elatius*, Ca – *Convolvulus arvensis*, Ce – *Cerastium arvense*, Cj – *Centaurea jacea*, Cs – *Centaurea scabiosa*, Cv – *Coronilla varia*, Dc – *Dianthus carthusianorum*, Ec – *Euphorbia cyparissias*, Fs – *Festuca rupicola*, Fv – *Fragaria viridis*, Ga – *Galium album*, Gv – *Galium verum*, Kp – *Koeleria pyramidata*, Lc – *Lotus corniculatus*, Ml – *Medicago lupulina*, Mo – *Melilotus officinalis*, Pa – *Poa angustifolia*, Pl – *Plantago lanceolata*, Pm – *Plantago media*, Pr – *Potentilla reptans*, Ps – *Pimpinella saxifraga*, Sm – *Sanguisorba minor*, Tc – *Trifolium campestre*, Te – *Teucrium chamaedrys*, Tp – *Thymus pulegioides*, Tr – *Trifolium repens*, Va – *Vicia angustifolia*, Vh – *Vicia hirsuta*, Vs – *Vicia tetrasperma*, Vt – *Vicia tenuifolia*.

Discussion

In most papers dealing with the species associations in the course of succession or on the disturbance gradient (Greig-Smith 1952, Kellman 1969, O'Connor and Aarssen 1987), attention is paid mainly to the frequency (total number standardized to the number of possible species pairs) of significant associations and its decrease in successionally late or undisturbed climax vegetation is usually found. In our study, we have not found a consistent trend in the frequency of significant associations, but in accordance with the

Table 3. Average values of the V coefficient for groups of species pairs belonging to particular life forms in the young field. Numbers of species in particular groups are given in parenthesis.

		annuals	biennials	perennial forbs
annuals	(19)	-0.017		
biennials	(2)	-0.018	-0.077	
perennial forbs	(5)	-0.010	0.004	-0.029

Monte Carlo test based on F-value: $P = 0.740$; Monte Carlo test based on difference between maximum and minimum: $P = 0.420$.

Table 4. Average values of the V coefficient for groups of species pairs belonging to particular life forms in the medium aged field. Numbers of species in particular groups are given in parenthesis.

		annuals	biennials	perennial grasses	perennial forbs
annuals	(7)	0.004			
biennials	(3)	-0.015	-0.031		
perennial grasses	(4)	-0.007	-0.030	-0.161	
perennial forbs	(10)	-0.014	-0.011	-0.024	-0.018

Monte Carlo test based on F-value: $P = 0.046$; Monte Carlo test based on difference between maximum and minimum: $P = 0.040$.

Table 5. Average values of the V coefficient for groups of species pairs belonging to particular life forms in the oldest field. Numbers of species in particular groups are given in parenthesis.

		annuals	perennial grasses	perennial forbs
annuals	(5)	0.036		
perennial grasses	(5)	-0.013	-0.048	
perennial forbs	(13)	-0.014	-0.022	-0.016

Monte Carlo test based on F-value: $P = 0.336$; Monte Carlo test based on difference between maximum and minimum: $P = 0.028$.

papers cited above, the minimum of associations was found in the mature forest. On the other hand, it seems that more information may be obtained, when the pattern of associations is analyzed with respect to life history of particular species.

In most cases, the number of significant associations is very low, close to the expected number of associations resulting from the Type I error (i.e. rejecting the null hypothesis

when it is true). However, manipulative experiments with selective herbicides carried out on the same plots (Michálek, Buriánek and Hadincová 1990) supported the hypothesis about strong competition between species. Particularly, the exclusion or suppression of one group of species led to an increase of abundance in unaffected (less affected) species. For example, the exclusion of dominant grasses (*Festuca rupicola, Poa angustifolia)* on the oldest field resulted in rapid spread and dominance of the species *Fragaria viridis*. This is evidence for competitive suppression of *Fragaria*. The value of V is -0.12 for *Fragaria* and *Festuca* and 0.13 for *Fragaria* and *Poa* (both non-significant). The estimation of pairwise competition effect from manipulative experiments and their subsequent comparison with V values is impossible as the herbicides influenced various species to various extents. The experiments were not designed to detect and measure competition, nevertheless their results suggest that competition plays an important role in shaping the community, despite the fact that only few significant negative associations were detected. However, the differences in morphology of *Poa* and *Festuca* indicate that *Fragaria* might be more competitively suppressed by *Festuca*, which has more compact tussocks.

The low frequency of negative associations determined from qualitative data may be partially caused by the low frequencies of species — the expected number of common occurences is then close to zero and the negative association is undetectable. However, the number of positive associations and the number of associations determined from quantitative data is low, too. This supports the idea of importance of diffuse competition in plant communities (Wilson and Keddy 1986).

Neither Rogers (1983), nor we in the present study found a pronounced relationship between phenological similarity of species and their association. Nevertheless, we have found, particularly in older successional stages, non-random patterns in species associations with regard to species life histories. Annuals are usually positively associated, whereas between strong perennial competitors negative associations prevail.

Conclusions

Following conclusions can be drawn:

1. No consistent trend was found in the frequency of significant associations with the successional age of the plot.
2. The hypothesis that species with similar phenology compete more and consequently are spatially segregated is only weakly supported by the data.
3. In older successional stages, differences were found in associations of species with respect to their life history types.
4. The frequency of significant associations may be considered neither as a measure of biological organization, nor as a measure of competition in the community.

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