COENOSES 10(1): 29-38, 1995
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APPLICATION OF THREE APPROACHES TO EVALUATE ABUNDANCE AND RARITY IN A SAND GRASSLAND COMMUNITY

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Keywords: C_4 and intermediate types of photosynthesis, Dominance, *Festucetum vaginatae,* Generalists, Mesophyll succulence, Net photosynthesis, Niche width, Overlap, Specialists, Water use efficiency.

Abstract. This paper gives an account of causal analyses of populations, which are sharply different in relative abundances in the perennial drought limited sand grassland *Festucetum vaginatae*. Three complementary approaches were pursued:
1. Sociological, based on spatial associations between species-pairs to find species sensitive or indifferent to the common ecological factors extracted by factor analysis.
2. "Traditional", rooted in niche theory using the parameters of niche width, and overlap between species in pairs and multiplets. All calculations were based on measurements of soil moisture content and depth of maximal root mass.
3. Experimental, involving investigations on the physiological tolerance and adaptation mechanisms of populations to interpret results obtained by approaches 1 and 2.
We found a positive relationship between abundance and niche width. The dominant species, *Festuca vaginata,* has the largest niche width and highest average overlap value. Regarding the role of species in niche space measurements concerning photosynthesis ecology and biochemistry indicate that the rank order of species based on mesophyll succulence is informative and that in continental open grassland communities with summer drought, species with C_4 and/or C_3 -C_4 intermediate photosynthesis type have the best chance to achieve competitive superiority in the role of a generalist.

Nomenclature: Soó (1980).

Abbreviations: P_n=net photosynthesis; R_D=dark respiration; S_M=mesophyll succulence; WUE=water use efficiency of net photosynthesis.

Introduction

The commonness and rarity of species strongly affect community diversity which, together with the distribution of relative species abundance, can be regarded as overall characteristics of community structure and organization (Gause 1936, May 1981). Raunkiaer's law of frequency entails yet another characteristic concerned with the unequivocal distribution of frequency categories in communities. Questions connected with these characteristics come up time to time in different contexts. The detection of similar pattern of abundance distributions at local to regional scales (Hanski 1982, Collins & Glenn 1991) is an example.

Our focus is on abundance and rarity. Abundance distributions reflect the partitioning of resources in a community (Giller 1984). The different distribution models reflect basic types of structure in niche space (Whittaker 1965, 1972; for review, see Magurran 1988). This "method" can be considered indirect because of its purely taxonomic basis. Experimental methods are more direct, since they rely upon *in situ* and *ex situ* measurements of environmental/ecological factors which affect species distributions, the niches of the species, or entire sets of species. Unfortunately, the methodological and theoretical gap between the direct and indirect approaches is wide.

In this paper analyses of species with sharply different abundances are presented. The uneven distribution of the individuals of various species is characteristic of the severe conditions in the Pannonian perennial sand grassland vegetation chosen for investigation. It is important from a practical point of view that under extreme conditions like ours, the influential ecological factors are generally reduced to a few. Our basic aim is to explain the observed pattern of species abundances with emphasis laid on outcome from different approaches as applied to the same set of objects. The three series of investigations are indeed complementary in specific respects. The phenomenological aspect, i.e., species composition is taken as a basis. Causal analyses are accomplished at two levels: by *in situ* study of the habitat niche (Cody

1986) and by *ex situ* study of the internal (physiological-biochemical) properties of the species.

Materials and methods

Community and species

The *Festucetum vaginatae danubiale* grassland is widely distributed throughout the Danube Basin, and as a "paraclimax" community it develops on loose calcareous sandy soils. This perennial grassland shows some semidesert characteristics for edaphic reasons. The present investigations were carried out in stands of this dry grassland community at Vácrátót (30 km NE of Budapest, 130 m a.s.l.). The mean annual precipitation is about 550 mm. The vegetation cover is maximum 50 to 60%, and the total species number is low (40 to 50 in a uniform stand 50 x 50 m^2 size). As to geographic distribution and life form, the constituent species are mainly continental, Pontic, Ponto-Pannonian hemicryptophytes, therophytes, but chamaephytes and geophytes also occur. A special feature is the presence of numerous endemic taxa characteristic of the habitat. This community is well-known to classical phytosociology (Magyar 1933, Hargitai 1940, Soó 1957 and others) and its vegetation dynamics has also been studied (Fekete et al. 1988, Fekete 1992). A detailed description of the species composition of the stand under study is presented in Kárpáti & Kárpáti (1954), and Fekete et al. (1976). Important information on the commonness and rarity of the species is given by Nosek (1986) who studied relative importances and constructed dominance-diversity curves for the community at different plot sizes.

Methods for analysing species composition

For description of the sociological behaviour of species, presence-absence data were collected from 100 quadrats 50 x 50 cm^2 each, placed along a line. In order of decreasing frequency (in parentheses) the species studied include: *Festuca vaginata* W. et K. (100), *Thymus* sp. *(72), Medicago minima* (L.) Grufbg. (63), *Euphorbia seguieriana* Necker (59), *Carex stenophylla* Wahlbg. (48), *Fumana procumbens* (Dun.) Green et Godr. (28), *Cynodon dactylon* (L.) Pers. (21), *Centaurea arenaria* M. B. (13), *Equisetum ramosissimum* Desf. (11). The data were used to compute a matrix of interspecific correlations. This matrix was analysed by the centroid method of factor analysis (Harman 1962, Lawley & Maxwell 1963). Three centroids were extracted and the communality and specificity values (Précsényi et al. 1980) of the species were calculated.

Niche investigations: field measurements and calculations

The moisture content of the soil was measured by a portable instrument operating on the basis of electrolyte conductivity. The electrodes were inserted into the soil at the rhyzosphere depth of the species examined. Conductivity values were directly read from the instrument in mS. After calibration on a series of sand samples with known water content, the relationship between the moisture content of the sand soil and conductivity, in the 0-10% range of relative moisture content, was linear. It should be noted that the actual water content reached a 3-4% maximum only after rain. During summer the soil moisture content is in the range of 1.1 - 3% of dry weight (Tuba 1984b). For plants the depth of maximal root mass was measured. This characteristic is important for the use and partitioning of resource space among species. For calculations the data were grouped into equidistant categories. It was shown that the expression of the parameters of the niche ("habitat-niche", sensu Grubb 1986) was more natural when the categories of factor combinations of soil moisture and the depth values were used instead of using separate axes. The measurements were carried out in summer (water shortage) and in autumn (good water supply) for the same set of plants. The average values of measurements carried out repeatedly in three consecutive days were taken into consideration. On the basis of frequency values found in the categories, the values of niche parameters (Horn 1966, Pielou 1972, Pianka 1972) were calculated: Shannon-formula for species niche width,

$$H_i = -\sum_{j=1}^{c} p_{ij} \log p_{ij}$$

where j=1 to c are the categories; Horn's formula (Horn 1966), for niche overlap:

$$R_{hi} = \frac{H_{obs} - H_{min}}{H_{max} - H_{min}}$$

where H_{obs}= observed, H_{min}= minimum, H_{max}= maximum entropy. This equation was used for the estimation of the overlap of two or more species.

Ecophysiological methods

The rate of CO_2 exchange - net photosynthesis (Pn) and dark respiration (Rd) - was measured with infrared gas-analyser (Infralyt 4, Junkauer Dessau) equipped with a Peltier-module, in an open system (Masarovicova, 1984) on intact plants in a controlled CO_2 exchange chamber (Szente et al. 1993a, b) at 1000 uE . $m^{-2}.s^{-1}$ photosynthetically active radiation (PAR) and 201 °C leaf temperature. Dark respiration was determined as the net CO_2 release 20 min after onset of illumination. Other conditions were the same as for the net photosynthesis measurements. In all cases steady-state net CO_2 uptake or release was measured under atmospheric gas conditions (340 $\mu mol.mol^{-1}$ CO_2, 21% O_2), while the flow rate through the chamber was maintained at 60 l^{h-1}. Transpiration rates were measured alongside the net CO_2-uptake, in the CO_2 (and water vapour) exchange chamber under controlled conditions according to Stocker (1929) as described by Nagy et al. (1993).

Water use efficiency (WUE) is the ratio of net photosynthesis to transpiration rate (Larcher 1980). The identification of types of photosynthesis was based on chloroplast ultrastructure (JEM 100C EM; Maróti, Tuba & Csík 1984), the activity of the carboxilase enzymes (Horánszky & H. Nagy 1977) and CO_2-exchange characteristics (Tuba in prep.). Chloroplast pigments (chlorophyll a and b, b carotene and xanthophylls) were measured as described by Tuba (1984a).

The mesophyll-succulence (S_M) index was calculated according to Kluge & Ting (1978). Measurements of all above physiological parameters were carried out in at least five repetitions.

Results

1. The sociological approach

Before taking the special measurements in niche space, the study of phytosociological affinities of species can help in formulating hypotheses. It is assumed here that the sociological relations of the species reflect their answers as it were to ecological factors. As an exploratory method, the centroid algorithm of factor analysis seemed to be an appropriate tool. The results of this are given in Table 1.

It is well-known (Harman 1962, Lawley & Maxwell 1963) that the communality value (h^2) of a variate (here: species) in centroid analysis represents the portion of the variance of the variate which is due to the common factors. *Festuca vaginata* and *Thymus* sp. have high communality values (so reflecting the existence of common causes). There is no difference in the loadings of these two species (Table 1). Interestingly, *Fumana procumbens* has the lowest communality and thus the highest specificity ($1\text{-}h^2$) value. So this species is not sensitive to common factors which affect the sand grassland. These and similar findings with other species suggest the existence of generalists and specialists in the community.

2. The approach using the niche concept

In the sand grassland communities in the Danube Basin, the most important environmental factor determining patterns and processes is water, the water regime of the soil. Szodfridt & Faragó (1968) clearly showed strong water dependence in the spatial distribution of plant communities. The water-controlled organic matter production in a perennial grassland on sand was documented by Kovács-Láng & Szabó (1971).

Based on the water-limitation concept, several studies dealt with niche partition in sand grassland. Some of them focused on the mathematical properties of various indices introduced for describing niche width and overlap (Fekete et al. 1976, Précsényi et al. 1977a, 1977b).

Niche width. Niche width is considered to be the most important parameter expressing the species' ability to acquire resources (Giller 1984). During summer drought, populations differ in niche width, while abundant water supply minimizes these differences in autumn (Table 2). Summer values show that the most abundant species in the community (*Festuca vaginata, Thymus* sp.) have the largest values of niche width (Table 2). At the other extreme, rare species like *Equisetum ramosissimum* and *Centaurea arenaria* proved to be specialists having narrower niche widths in summer. This separation of generalists and specialists shows a trend similar to that shown by the centroid analysis.

Table 1. The centroid loadings, communality (h^2) and specificity values ($1\text{-}h^2$) of species.

Species	Loadings				
	I.	II.	III.	h^2	$1\text{-}h^2$
Festuca vaginata	0.84	0.37	0.09	0.85	0.15
Medicago minima	0.78	0.30	-0.07	0.70	0.30
Thymus sp.	0.84	0.38	0.14	0.87	0.13
Euphorbia seguieriana	0.66	-0.14	0.19	0.49	0.51
Carex stenophylla	0.79	0.08	-0.08	0.64	0.36
Fumana procumbens	0.30	0.07	-0.13	0.11	0.89
Equisetum ramosissimum	0.40	-0.36	-0.08	0.30	0.70
Cynodon dactylon	0.61	-0.05	0.17	0.40	0.60
Centaurea arenaria	0.40	-0.62	-0.33	0.65	0.35

Table 2. Niche width (combination of soil moisture content and root depth) in H values.

Species	Summer	Autumn
Festuca vaginata	0.677	0.615
Medicago minima	0.527	0.623
Thymus sp.	0.664	0.508
Euphorbia seguieriana	0.666	0.652
Carex stenophylla	0.588	0.549
Fumana procumbens	0.510	0.543
Equisetum ramosissimum	0.323	0.587
Cynodon dactylon	0.414	0.462
Centaurea arenaria	0.341	0.543

The expressed seasonality (shift of averages) can also be seen in Figure 1, where niche centres (mean values) are shown. Here two separate axes were used for representation. The distance between summer and autumn niche centres is significant, while the relative positions of species remain similar. Furthermore, an uneven distribution of averages can be observed. This may have two possible explanations: 1) The distribution of resource categories is even but that of the species is uneven; 2) The distribution of resource categories is uneven. In our opinion it is more logical to operate with the summer data set which represents a water shortage condition characteristic of the overwhelming part of the vegetation season.

Niche overlap. Overlap values (Table 3) greatly vary. The one extreme is represented by *Fumana* with low or, in the majority of cases, zero overlap. Its opposite is *Festuca vaginata*. The distinction of species according to their over-

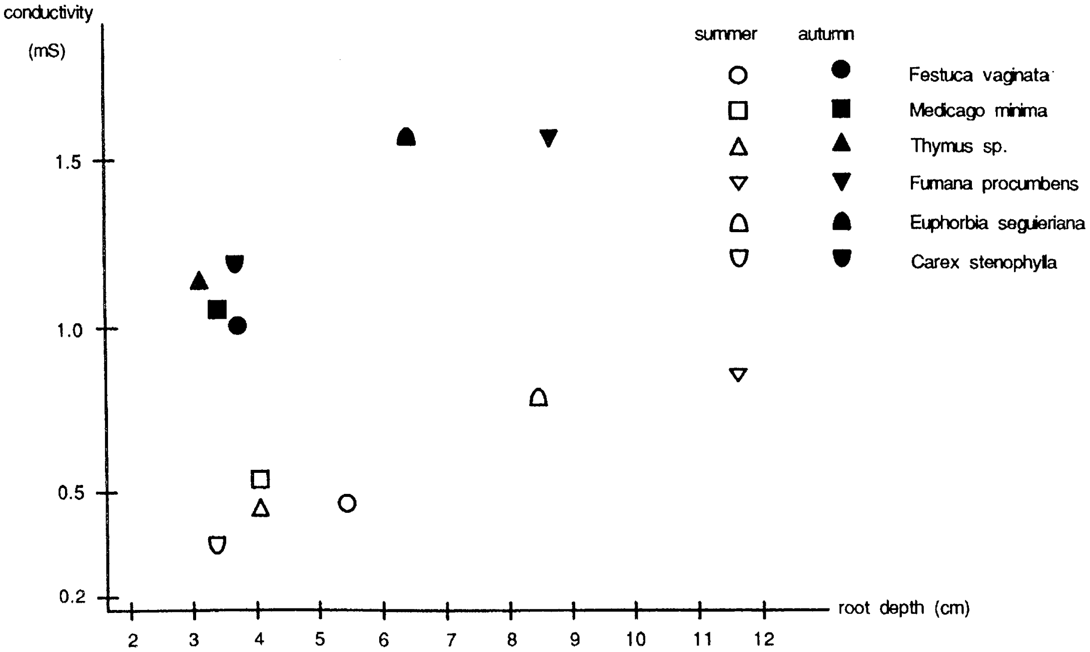

Figure 1. Position of niche centres related to root depth (cm) and soil moisture content (in terms of conductivity, mS=milli-Siemens) in summer and autumn.

laps is noteworthy: *Festuca*, *Medicago* and *Thymus*, the first three species in the abundance rank order, overlap considerably. The pairwise overlap in the group of the subordinate or rare species (*Fumana*, *Cynodon*, *Equisetum*, and *Centaurea*) is generally low or very low (with one exception).

The relation between niche width and niche overlap is hardly known. A general trend is suggested by the summer results in Figure 2, namely, the larger the niche width the larger the average niche overlap (the average of a given species with the eight other species).

The pairwise overlaps represent only special cases of niche analysis. Horn's index (Horn 1966) is a good means of measuring niche overlap between species pairs and among multiple species. The values of all the cases (from all possible species pairs to the only possible combination of nine species) have been calculated. Here only the averages of individual groups (pairs, triplets, etc.) are presented in Figure 3 (summer data set). The averages of overlap for species combinations with and without the generalist *Festuca vaginata* (*Festuca*$^{+}$ and *Festuca*$^{-}$) are also shown. The same procedure was repeated with *Fumana*, which is considered to be the other extreme (specialist). The *Festuca*$^{+}$ curve is flat because *Festuca* overlaps with other species to the same ex-

Table 3. Niche overlap values (R$_{hi}$), according to the combination of soil moisture and root depth. Summer values

	Medicago minima	*Thymus* sp.	*Euphorbia seguieriana*	*Carex stenophylla*	*Fumana procumbens*	*Equisetum ramsissimum*	*Cynodon dactylon*	*Centaurea arenaria*
Festuca vaginata	0.421	0.645	0.370	0.520	0.069	0.769	0.638	0.643
Medicago. minima		0.642	0.088	0.623	0.000	0.521	0.455	0.185
Thymus sp.			0.120	0.654	0.000	0.579	0.505	0.254
Euphorbia seguieriana				0.216	0.648	0.159	0.000	0.381
Carex stenophylla					0.000	0.538	0.279	0.191
Fumana procumbens						0.000	0.140	0.000
Equisetum ramosissimum							0.673	0.000
Cynodon dactylon								0.262

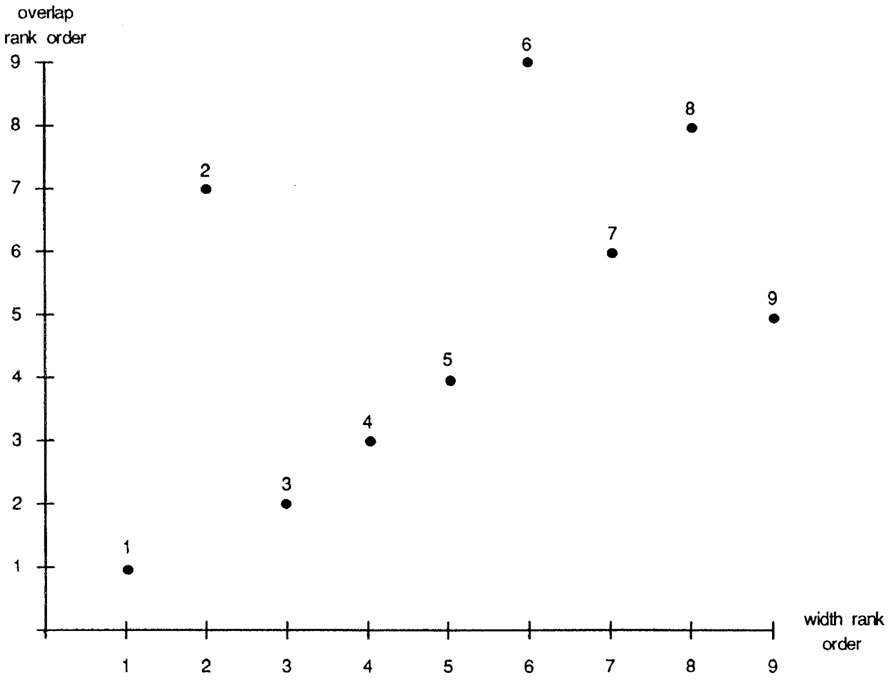

Figure 2. Relation between rank order of niche width (H) and average overlap (R_{hi}) of species, according to combined categories. Summer situation: ***1 - Festuca vaginata, 2 - Euphorbia seguieriana, 3 - Thymus* sp., *4 - Carex stenophylla, 5 - Medicago minima, 6 - Fumana procumbens, 7 - Cynodon dactylon, 8 - Centaurea arenaria, 9 - Equisetum ramosissimum.***

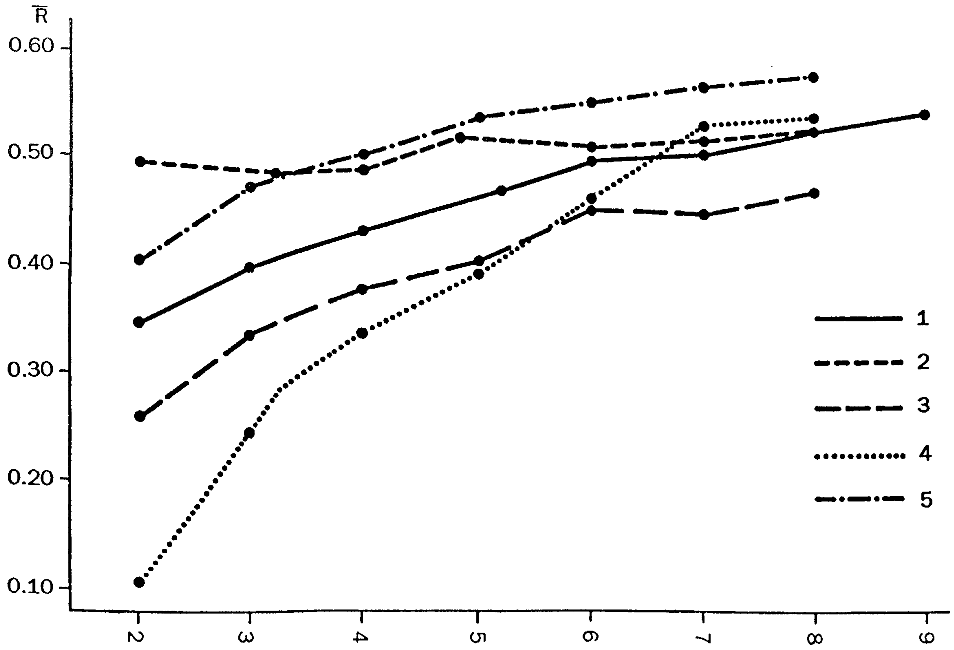

Figure 3. Averages of Horn's index for groups of species multiplets (pairs, triplets, etc.). 1 - Overlap averages of all species, 2 - of *Festuca*$^+$ groups, 3 - of *Festuca*$^-$ groups, 4 - of *Fumana*$^+$ groups, 5 - of *Fumana*$^-$ groups.

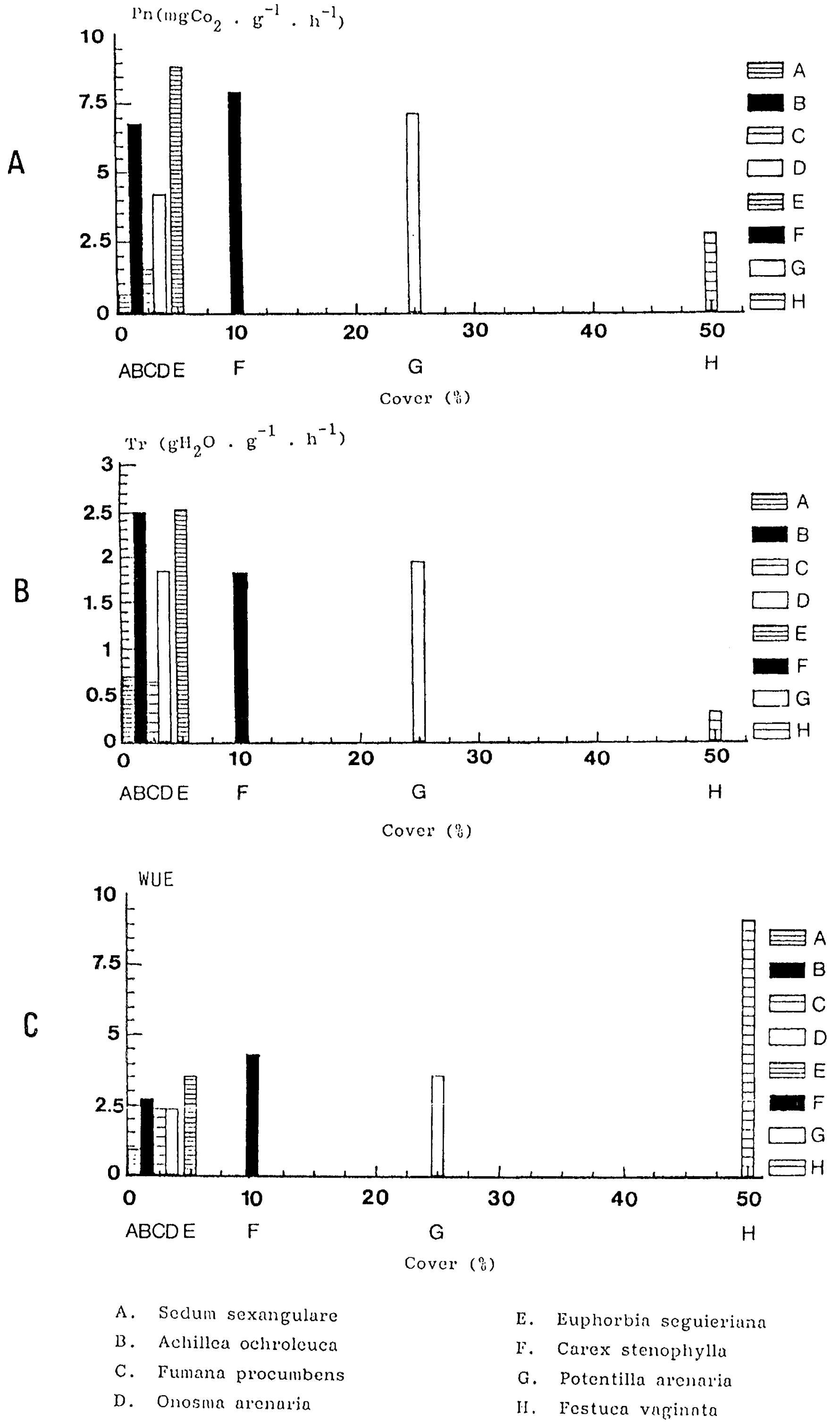

Figure 4. Maximal net photosynthetic intensity (A), transpiration rate (B) and water use efficiency of net photosynthesis (C) and percentage cover values of species of *Festucetum vaginatae* in the summer drought period (10 - 13. 7. 1984).

tent in the species pairs and triplets as at higher ranks. This characteristic of *Festuca* may be essential in understanding its ability to form a community. The ecological separation of *Fumana* is also well demonstrated in Figure 3.

A monotonic increase of the averages based on all possible species combinations is a fact. The overall niche overlap (combination of 9 species) is 50%. It is not certain whether this overall overlap has special significance in characterizing the plant community.

3. The ecophysiological approach

An important objective of this study was to find the factors governing the abundance of the species in the community. It may be assumed that photosynthetic capacity (rate of CO_2 incorporation) might explain phytosociological dominance. This assumption is based on the hypothesis that more aboveground and belowground phytomass is produced by the more competitive species. The results in Figure 4 do not support this idea. Species with low cover have higher photosynthesis rates than the dominant *Festuca vaginata*. The calculation of water use efficiency (WUE) gives different results. Figure 4 also shows that *Festuca vaginata* has the highest summer water efficiency (WUE). *Festuca vaginata* had a lower ratio of photosynthesis to dark respiration (R_D rate) and higher P_n/R_D ratio (during summer typical in the range of 4.8 - 6.1) than the other species (with a P_n/R_D value below 4.5, Tuba 1984b). The low mitochondrial respiratory activity of this species is important. This type of economic photosynthetic behaviour of *Festuca vaginata* may be the cause of its dominance.

A broad view is provided by Table 4 which summarizes the role of different biochemical pathways of photosynthesis for 34 species. Almost 50% of the species differ from a "typical" plant using only the Calvin-cycle. The dominant and codominant species of the community studied (*Festuca vaginata, Carex stenophylla*) belong to the intermediate C_3-C_4 type. These plants have adaptive and competitive superiority when fluctuation in water supply occurs. The high number of species with special biochemical pathways stresses the fact that in sand grassland water economy must have an influential role not only in water uptake, but also in the photosynthetic structure. Further details are found in Horánszky & H. Nagy (1977), H. Nagy & Horánszky (1980).

Another aspect of photosynthetic structure, photosynthetic pigment composition, of this community was also studied (Tuba 1984c). The quantities of 7 pigments (chlorophyll-a, chlorophyll-b, carotenoids: beta-carotene, lutein + zeaxanthin, antheraxanthin, violaxanthin, neoxanthin), were determined. The similarities of species (product moment correlation coefficient) were calculated on the basis of concentration values and 5 pigment ratios. Figure 5 shows the pigment structure of the community based on the group average clustering algorithm (Orlóci 1978). The separation of two sclerophyllous, C_4 (C_3-C_4) type species (*Festuca vaginata, Cynodon dactylon*) from the others is apparent (right side of the dendrogram). The two microphyllous sclerophylls (*Thymus* sp., *Potentilla arenaria*) are similar. In the middle of the dendogram a group of 4 malacophyllous, deep-rooting species (*Euphorbia seguieriana, Alkanna tinctoria, Onosma arenaria, Achillea ochroleuca*) can be seen. The two succulent species (*Sedum sexangulare, Fumana procumbens*) form a distinct group of specialists. These results suggest that the species with similar pigment

Table 4. Photosynthesis types of the species in sand grassland community on the basis of the activity of two carboxilation enzymes RuBP-c and PEP-c (principally after Horánszky & H. Nagy 1977, H. Nagy & Horánszky 1980). A: C_3, B: C_4, C: CAM-type.

Achillea collina	A	*Festuca vaginata*	A B
Achillea ochroleuca	A	*Festuca wagneri*	B
Anthemis ruthenica	A	*Holoschoenus romanus*	A
Bothriochloa ischaemum	B	*Koeleria majoriflora*	B
Carex liparicarpos	A	*Onosma arenarium*	A
Carex praecox	A B	*Phleum phleoides*	B
Carex stenophylla	A B	*Plantago indica*	A
Centaurea arenaria	A	*Poa angustifolia*	B
Crepis rhoeadifolia	A	*Poa bulbosa*	A B
Cynodon dactylon	B	*Potentilla arenaria*	A
Cynoglossum hungaricum	A	*Potentilla impolita*	A
Digitaria sanguinalis	B	*Scleranthus annuus*	B
Equisetum ramosissimum	A	*Sedum acre*	A C
Erigeron canadensis	A	*Sedum sexangulare*	A C
Eryngium campestre	A	*Silene otites*	B
Erysimum canescens	A	*Sisymbrium altissimum*	A
Euphorbia seguieriana	A	*Stipa borysthenica*	B

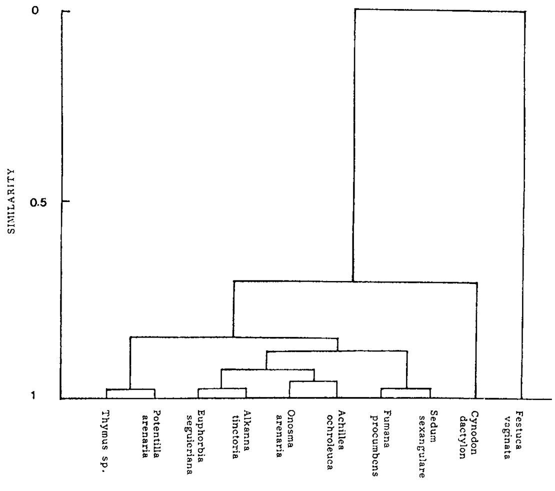

Figure 5. Dendrogram of cluster analysis (group average algorithm, Orlóci 1987) based on the similarity matrix of pigment composition of species in *Festucetum vaginatae*. Summer drought period, 1983.

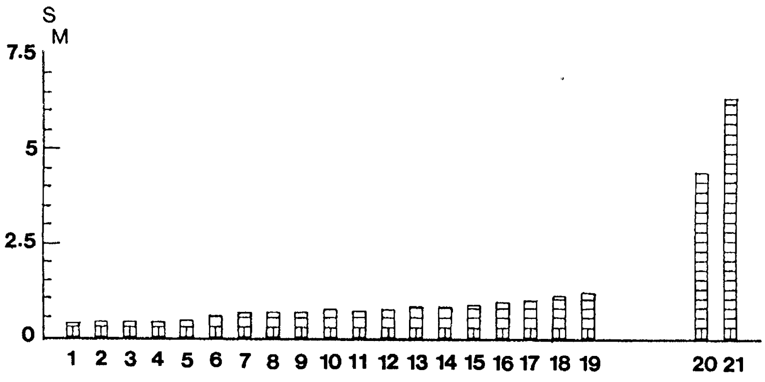

Figure 6. Mesophyll succulence (S_M) relations of the species in sand grassland community (2 - 15. 8. 1984).

$$S_m = \frac{\text{water content } (g\ H_2O\ .\ g^{-1} fr.\ w.)}{\text{total chlorophyll content } (mg\ Chl\ a+b\ .\ g^{-1}\ fr.\ w.)}$$

1. Stipa joannis
2. Bothriochloa ischaemum
3. Cynodon dactylon
4. Festuca vaginata
5. Carex stenophylla
6. Koeleria glauca
7. Potentilla arenaria
8. Potentilla argentea
9. Salvia nemorosa
10. Conyza canadensis
11. Polygonum arenarium
12. Thymus sp.
13. Euphorbia seguieriana
14. Alkanna tinctoria
15. Achillea ochroleuca
16. Veronica spicata
17. Onosma arenaria
18. Fumana procumbens
19. Plantago indica
20. Sedum sexangulare
21. Sedum acre

composition have similar water economy as well. In other words, biochemical-physiological and morphological types reflect closely the water economy.

We conclude that water ecology is crucial in determining the role of species within this community. In order to characterize water ecology of these species on a common basis, the mesophyll succulence index (Kluge & Ting 1978) is used. This index expresses a ratio of water content of mesophyll tissue to chlorophyll content. Since the latter is proportional to the volume of the mesophyll tissue, by using this index the distortion caused by the varying proportion of nonassimilating tissues in different species can be excluded.

Although the results in Figure 6 give a rather continuous spectrum (except for the two *Sedum species*), the sequence of the species is interpretable. A series of sclerophyllous (spp. 1-6) - sclerophylloid (spp. 7-12) - malacophyllous (spp. 13-17) - succulent (spp. 18-21) species can be detected. The species of different biochemical characteristics, namely C_4 (C_3-C_4) - from *Stipa* to *Koeleria* - and CAM species are situated at the extremes of this series, which also means the separation of generalists. *Festuca vaginata,* a generalist according to its sociological properties (Table 1) and niche parameters, occurs at the beginning of the mesophyll succulence continuum, while *Fumana procumbens* (a specialist regarding its sociology and position in the niche space) is placed at the end. The maximal specialisation is represented by the two succulents: *Sedum sexangulare* and *S. acre*. Despite the continuous spectrum, there was no overlap between any species pairs.

Discussion

The opinion of ecologists in the use of the niche concept in plant ecological studies is not unequivocal. Watkins & Wilson (1992) documented "niche limitation" (decrease in the variance of species richness indicating limitation to the potential niches) at a small spatial scale (see also Wilson, Roxburgh & Watkins 1992). Whereas van der Maarel & Sykes (1993), studying the "alvar" limestone grassland question the usefulness of the niche concept. They were able to document that each microsite may be colonized by any of the grassland species and therefore - as they state - "all species of the plant community have the same habitat niche". For describing plant species turnover a new model (the "carousel model") was suggested. Persistence, the longer existence of the same plant individual on the same place, is, however, by no means excluded even in the case of the alvar limestone grassland (as shown by Fig. 2). We suggest that persistence is more characteristic of communities with a low level of competition like in the *Festucetum vaginatae*. A main question is the speed of change, the time needed for a turn-over cycle. Persistence should be regarded important also as a condition for an equilibrium state between plant and environment that ensures the reliability of the environmental measurements. We hypothesize that in dry sand grassland the number of responsible ecological factors is reduced (compared to limestone grassland with xeromesic habitat).

There are only a few papers describing all or at least a set of species characteristic of a community in terms of the niche concept. Even fewer studies address physiological properties of plants (Bazzaz 1979, Zangerl & Bazzaz 1983, etc.). Recently, Lösch (1990) has been working intensively on the water relations and photosynthesis background of niche properties. Nevertheless, our study is among the few in which particular attention is paid to linking two types of investigations: *in situ* environmental measurements and analyses of physiological properties, concerning the dominants and rare, characteristic species in a community.

Nosek (1986) demonstrated the stable dominance structure of the perennial sand grassland. The rank order of species is independent of the size of the basic sample unit (between 100 and 25600 cm^2). According to the shape of all dominance-diversity curves the distribution is lognormal, nearly to geometrical. At every size of the sample plot, *Festuca vaginata* is predominant, *Thymus* sp., *Medicago minima, Carex stenophylla* are subordinate. *Fumana procumbens* was found as subordinate or rare, *Cynodon* and *Centaurea arenaria* (and others) as rare. Our results concur with Nosek (1986) when niche width rank orders are concerned. On the other hand, if the sizes of niches (Table 2) are compared the maximum niche width is only twice as large as that of the smallest. This is considerably different compared with the abundances of species, for which magnitude differences also exist. Nevertheless, we distinguished between generalist and specialist populations in the sand grassland. We emphasise that these findings on specialist or generalist behaviour are relative, and have validity only in the framework of the community studied. To formulate hypotheses in this respect, the role of special sociological pre-investigations (like centroid analysis) should be underlined. It seems that the absolute dominance of *Festuca vaginata* in the community is related to its large niche width.

The fact that the Pannonian perennial sand grassland has a well-defined species composition with fixed abundance ratios is supported by long term observations. Despite the high level of the overlap found for numerous species pairs in the dimensions chosen in the present study, a stable coexistence is indicated. There are no unidirectional competitive exclusions between the species studied. Considering overlap, the behaviour of species is not uniform and at least two groups can be distinguished. The first group is formed by specialists with narrow niche width and low average overlap (especially low intra-group overlaps) and with better segregation (especially for *Fumana*). Generalist species exhibit higher overlap (as indicated by the high intra-group overlap values) and the niche-centres are similar. This resembles a limestone grassland where coexistence was found in the absence of niche differentiation (Mahdi et al. 1989). We suppose that niche diversification takes place possibly in further dimensions at least for the generalists. Time as a factor responsible for segregation should be taken into consideration ("phenological niche", sensu Grubb 1986). Although much is known about the late autumn and early spring phenology in this grassland (Kárpáti & Kárpáti 1954), the temporal activity of subterranean interactions is poorly understood.

The positive correlation between niche width and overlap has been rarely documented. Zaret & Rand (1971), for example, described a change from small non-overlapping food niches in nutrient poor season to broadly overlapping niches in a more productive environment for fish species in tropical streams.

To explain the behaviour of generalists and specialists some physiological properties were emphasized. It appeared that there is no connection between the area covered by a plant species and its net photosynthetic capacity. However, a positive relationship exists between net photosynthetic efficiency and abundance. Both photosynthetic pathways (C_4, CAM) allow the survival of species in this community, but their relative success is different. In continental edaphic semideserts like the Hungarian ones, succulents cannot achieve dominance, they are able to fill only special parts of the community niche space. The best way of surviving summer droughts and becoming a competitively superior generalist is to have a C_4 or C_3-C_4 intermediate type of CO_2 assimilation. This characteristic of some grass species is connected with sclerophyllism. We could demonstrate that every species in the community made full use of the possibilities of succulence. The range of mesophyll succulence scale can be considered as a characteristic parameter for the community.

Acknowledgements. The present work was supported by the Hungarian Scientific Research Foundation (OTKA 3/936, 1/848 and 3/1545).

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Manuscript received: May 1995