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ON THE STRUCTURE OF THE PANNONIAN FOREST STEPPE: GRASSLANDS ON SAND

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The paper discusses the floristic and coenological structure of the Pannonian part of the Eurasian forest steppe biome. The vegetation of the sand landscapes of the Hungarian lowlands is examined where a climate gradient was detected with decreasing annual precipitation from NW to SE. For studying the effect of the gradient, sites in three different sand landscapes were selected. With increasing aridity, semidesert-like communities become dominant and the steppe grassland, *Festucetum wagneri* loses almost all of its steppe characteristic. Among the soil factors it is the organic matter content that explains the closed steppe-open grassland trend. The chorological analysis of the forest and steppe grassland species does not support – despite previous expectations – an opposite distributional trend for the two groups.

Key words: climate gradient, forest and steppe flora gradient, landscape mosaic, raster vegetation map

INTRODUCTION

The forest steppe can be defined as a separate vegetation belt developed in the transitional climate between the zones of closed forests and steppe grasslands. In this belt, more or less closed forests alternate with closed grasslands, forming a landscape of mosaic appearance (WALTER 1943, BERG 1958). Abiotic conditions, herbivores, and fires together are responsible for this mosaic determining whether at a given locality forest or grassland appears.

The zone of the forest steppe is extensive and runs in Eurasia from the Pannonian lowland to China. During its history, the Pannonian part of this belt used to be in close connection with other parts of the zone through flora corridors. At present it is isolated from those. The great richness of this biome is affected by the several landscapes of the Carpathian Basin as documented by the extensive floristic and geobotanical literature.

Due to the transitional climate of this belt, a late summer-early autumn semiarid period lasts for at least two months in certain years (VARGA *et al.* 2000). Recently, statistical analysis showed that the climate of the Pannonian forest steppe is far from being uniform. In the Great Hungarian Plain, e.g., in the Duna–Tisza Interfluve (the area between the Danube and Tisza rivers) a NW–SE climate gradient exists (BORHIDI 1993).

Accordingly, vegetation scientists should question whether the effect of the climate gradient manifests itself in the vegetation, and if so, how (cf. KOVÁCS-LÁNG *et al.* 1999). As the gradient intersects the forest steppe belt, one may get insights into the structure of this biome as well.

First, the forest component of the zone was investigated. As the forest stands remained few in number, instead of studying the gradient in forest structure, the individual distributional data of forest species was examined (FEKETE *et al.* 1999). A conclusion was reached that there is a common trend in the distribution of forest trees, shrubs and understorey species in the Danube–Tisza Interfluve. The chorological pictures reveal an unequivocal diminishing of forest flora from north to south. Two different phenomena appear here simultaneously: both the number and abundance of forest species decreases continuously to the south.

In this paper the grassland component of the mosaic will be analyzed and discussed.

MATERIAL AND FIELD METHODS

Among the abiotic conditions influencing the formation of the vegetation pattern of this zone, the substrate has one of the strongest impacts. Two kinds of substrate, loess and sand are widely distributed in the interior of the Carpathian Basin. The vegetation on loess is generally of higher productivity. Continuous natural vegetation is rarely to be found here as agrarians have been cutting down the forests and breaking up the fields since the early postglacial times. In the semiarid climate, sand is less favorable for vegetation far from the water table. Productivity of herbaceous sand vegetation is particularly low on moving sand, where, for edaphic reasons, semidesert-like open grasslands occur as well. One can meet on sand, even today, larger patches of semi-natural vegetation. This was the reason for carrying out the experiments on sandy vegetation, particularly on the vegetation of calcareous rough sand in the Small and Great Hungarian Plains.

In the Hungarian plains, numerous sand landscapes isolated at present from one another by agricultural fields, settlements etc. are known to still bear more or less natural vegetation. In the course of a 4-year period, a number of sand landscapes were visited, where sites more or less characteristic of the given area, were selected. These sites were investigated using the same design and sampling methods. Studying the possible effect of the climate gradient, three sites (situated at the two opposite ends and at the middle of the gradient) were chosen for evaluation and comparison. For Site 1 a landscape in the Small Hungarian Plain was chosen, while the two other sites are situated in the Great Hungarian Plain (Fig. 1). (Distances: Site 1-Site 2: 128, Site 2–Site 3: 52, Site 1-Site 3: 148 kilometers.) In the landscapes, the place of the studied plots of 2 hectares was selected with the help of colored or black and white aerial photos. At each plot, a grid was created of 14 columns and 7 rows, altogether with 98 raster cells. In this way, one cell of the given grid covered 14 m × 14 m. Vegetation maps were created with the help of two different methods. First, coenological relevés of 1 m^2 quadrats were completed in each raster cell, along with 49 point measurements of soil quality parameters. In order to create a "traditional" map, the relevés were classified by the Zurich-Montpellier method, then a given cell – 14 m × 14 m – of the grid was qualified according to the relevé situated inside it. In this way vegetation maps – so-called raster vegetation maps (DIERSCHKE 1994) – were prepared. In accordance with the second method, releveès were also classified by numerical methods (multivariate analysis), and the results of the classification were reallocated into the grid, and vegetation maps were also developed this way. The novelty in the methods described above lies in the use of vegetation maps prepared in a standard and repeatable way. It seems reasonable to compare the whole mosaic of the vegetation, not only the individual plant communities separately. In the comparisons, special attention was paid to the steppe plants.

RESULTS

The climate gradient

This was defined by the change in level of precipitation as one of the main factors that form the abiotic and water-limited sand vegetation. Data from the meteorological stations closest to the study areas were obtained. There were five categories, based on precipitation levels. Proportions of each category at the meteorological stations are shown in Figure 2. Years with high rainfall (701–800 mm) decrease from NW to SE. In parallel to this, dry years (300–400 mm and 401–500 mm) increase. The share of years characterized by moderate precipitation amounts (501–600 mm) shows a uniform, explicit growing tendency. It has to be empha-

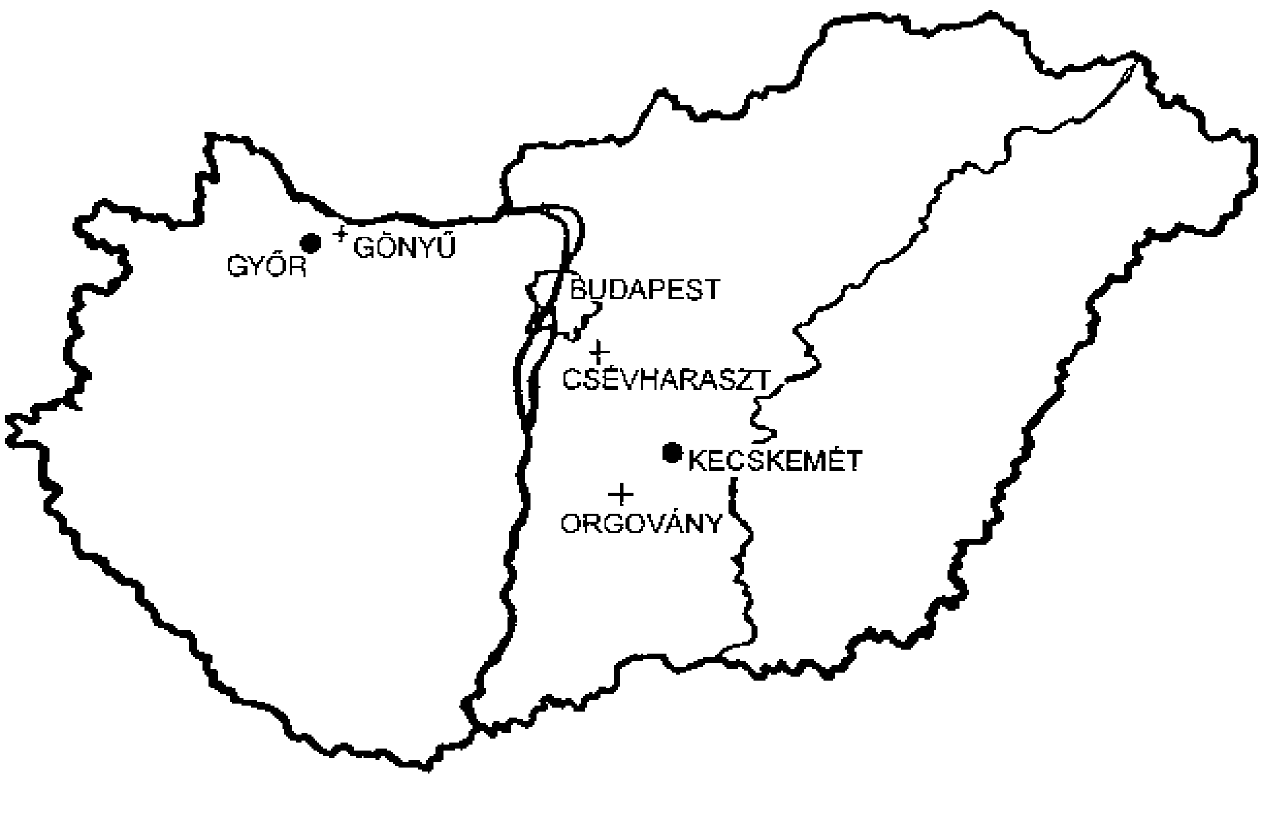


Fig. 1. The geographical position of the three sites. Site 1: Gönyű, Site 2: Csévharaszt, Site 3: Orgovány

sized that in case of years with low or moderate precipitation amounts, the warm summer period is the driest (cf. ZÓLYOMI *et al.* 1997, KUN 2000). According to the so-called semiaridity water deficit index (where the monthly amount of the precipitation and the monthly mean temperature above 0°C are taken into consideration), the number of semiarid years grows towards south-west (BORHIDI 1993).

Vegetation maps

Maps based on the traditional concept. Figure 3 presents the vegetation maps of the three sites based on classical concept. It has to be recalled that in this case, dominant and characteristic species were preferred for the identification of the communities. Regarding all the vegetation maps, 7 units representing herbaceous communities and 4 units representing scrubs (or forest) were distinguished.

Generally, perennial grasslands cover the areas. Their two contrasting groups are open semidesert-like perennial grasslands, and semiclosed-closed steppe grasslands. In the first group, the Pannonian endemic *Festuca vaginata* dominates. *Festucetum vaginatae* (1) is composed of perennial bunchgrasses such as *F. vaginata, Stipa borysthenica, Koeleria glauca* mixed with perennial herbs like *Euphorbia seguieriana, Alkanna tinctoria, Fumana procumbens* and has a sparse plant canopy covering 50–60 % of the soil surface. In the gaps, winter and spring annuals regularly occur. In some situations *Festuca vaginata* stands are mixed

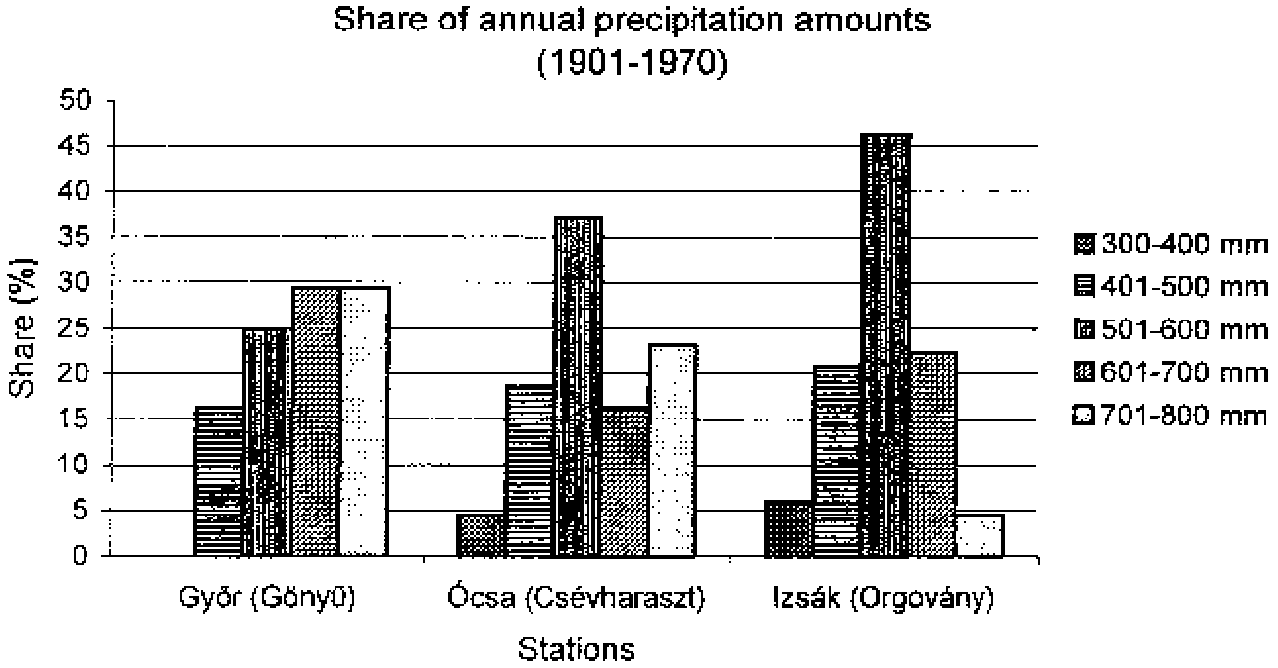


Fig. 2. Share of the categories of annual precipitation amounts (1901–1970) at the meteorological stations close to the study areas

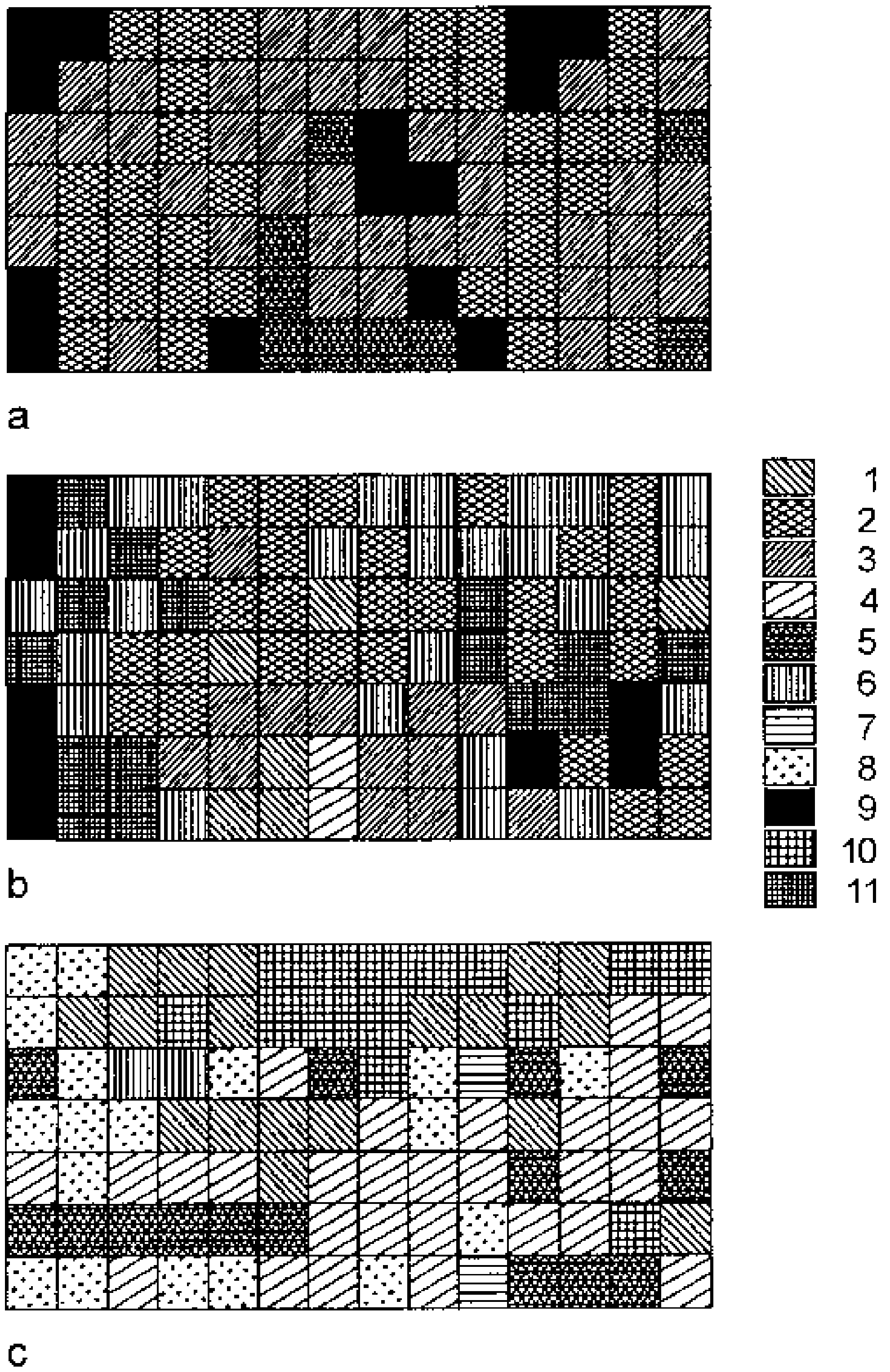


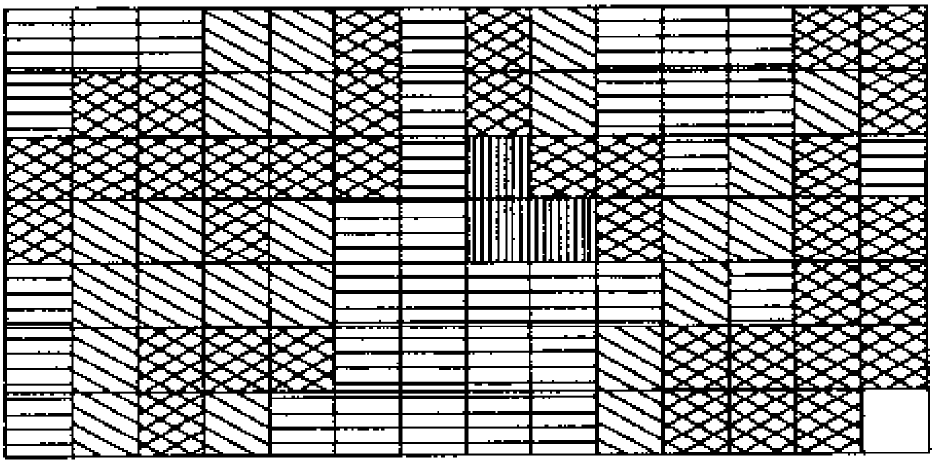
Fig. 3. The traditional vegetation maps of the three sites (a: site 1; b: site 2; c: site3). The vegetation units: 1 = Festucetum vaginatae (open perennial semidesert-like grassland); 2 = *Festuca vaginata* grassland with closed steppe elements; 3 = *Festucetum wagneri* (semi-closed steppe grassland); 4 = *Festucetum wagneri* grassland, species-poor; 5 = Meadow steppe (developed from wet meadow); 6 = *Poa angustifolia* steppe grassland (fringe community); 7 = *Salix rosmarinifolia–Holoschoenus romanus* wet meadow; 8 = Moss- and lichen-rich annual grassland; 9 = Forests (*Quercus robur, Populus alba, Robinia*); 10 = *Junipero-Populetum, Juniperus* scrub; 11 = *Crataegus monogyna–Ligustrum vulgare* scrub

with elements characteristic of steppe grasslands (2). In the group of the closed-semiclosed steppe grasslands four units occur. In most cases *Festuca wagneri* dominates, in the sward having coverage of 70(–80)%. The elements of the open grassland are depressed and their place is occupied by numerous steppe plants (e.g., *Phleum phleoides, Falcaria vulgaris, Eryngium campestre, Pseudolysimachion spicatum,* etc., (3). As in the case of *Festuca vaginata* grasslands, even with *Festuca wagneri* grasslands two types are developed (4: a unit poor in steppe plants). At the fringes of scrubs a loose sward of *Poa angustifolia* may develop (6). Finally, in interdune depressions in a state of drying up, a fourth unit called secondary meadow steppe was distinguished (5). For the further vegetation units see Fig. 3.

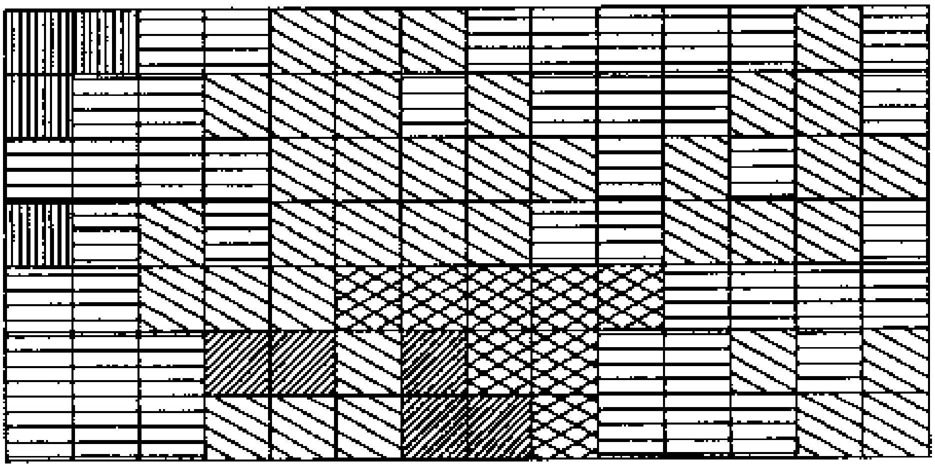
Considering the maps (Fig. 3) at Site 1 (Gönyű) it was observed that the steppe plants penetrate into the *Festuca vaginata*-dominated open perennial grassland as well. This community, together with *Festucetum wagneri* (rich in steppe elements) form large continuous patches. At Site 2 (Csévharaszt) influenced by *Festuca wagneri* steppe grasslands, shrubs and forests, the open perennial grassland allows some steppe plants in the majority of quadrats. As a difference, in comparison with Site 1 also *Poa angustifolia* dry grassland appears at the *Crataegus–Ligustrum* fringes. At Site 3 (Orgovány), steppe plants withdraw almost exclusively into the secondary meadow steppe. *Festuca vaginata* grassland does not contain such elements, the floristic composition of *Festucetum vaginatae* and *Festucetum wagneri* become very similar to each other. The extreme dry situation is indicated by the considerable extent of moss and lichen-rich annual grassland.

Maps based on multivariate analysis. There are other possibilities for visualizing the spatial vegetation structure of the three areas. First, the similarities between relevés can be calculated. Using these values, a clustering process may be applied and denoting and reallocating the relevés belonging to the same clusters, a new map can be constructed. Figure 4 depicts similarity maps based on species cover data. Here the similarity ratio (ROHLF 1963) was calculated using transformed cover values, and then the UPGMA (unweighted average linkage) clustering process (VAN DER MAAREL 1979) was applied. A given sign on the map indicates objects belonging to the same cluster. Figure 5 displays maps according to the presence-absence values, here the similarities were calculated by the Sørensen-formula (PODANI 1994), the further procedure is the same as in the former case.

Regarding the dominant-subdominant plant communities, similarity-vegetation maps of Site 1 and 2 resemble one another, while the separation of the third site from both sites is conspicuous (Fig. 4). Compared with the traditional vegetation map, the *Festuca vaginata* dominated grassland and *Festucetum wagneri* grassland separate more or less from one another at Site 1. At Site 2, the pattern of



a



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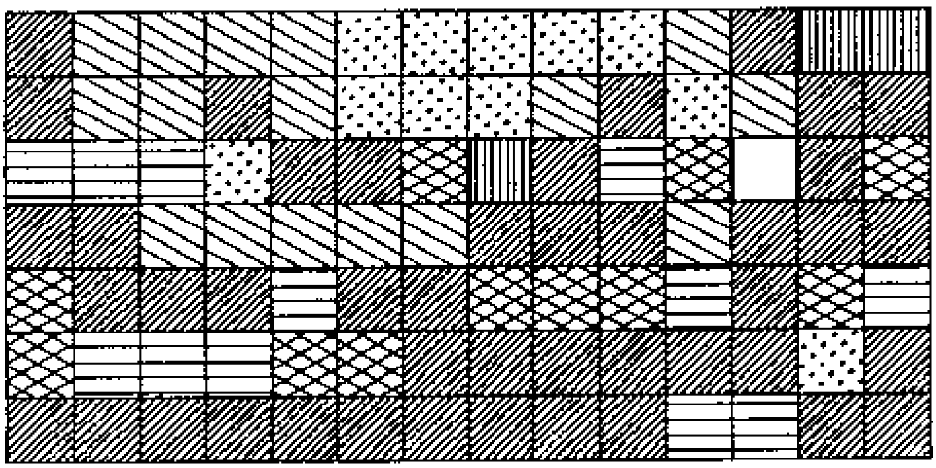

c

Fig. 4. Raster vegetation map. Similarities among relevés were calculated – based on cover data – by similarity ratio. a) Gönyű, b) Csévharaszt, c) Orgovány. For the details see the text

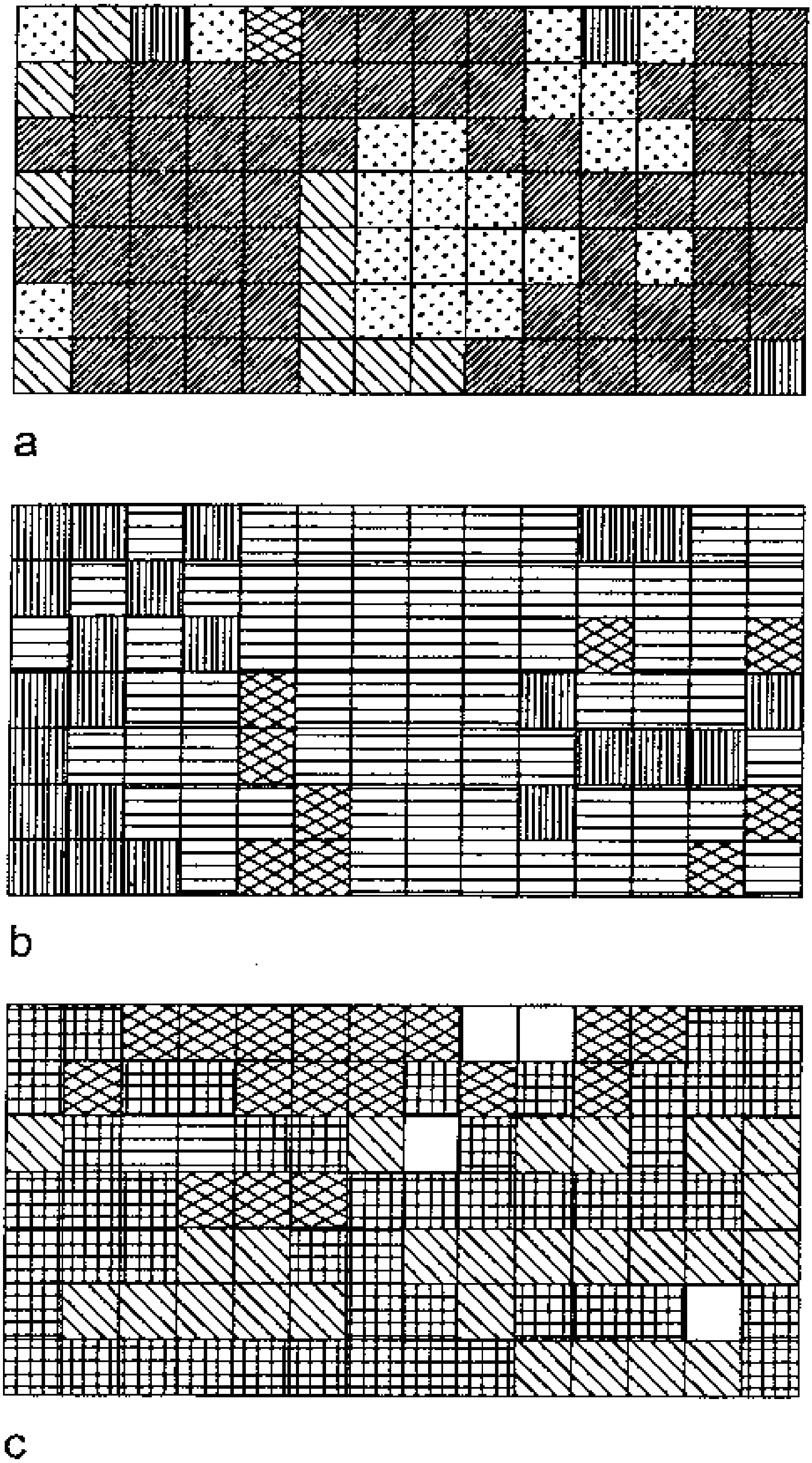

Fig. 5. Raster vegetation map. Similarities among relevés were calculated – based on presence-absence data – by the Sørensen formula. a) Gönyű, b) Csévharaszt, c) Orgovány

steppe-type *Festucetum vaginatae* can be identified, however, the shape of the patches of *Festucetum wagneri* is not outlined. Its quadrats break up into four groups. This community shows similarity in 7 quadrats with Site 1, while relation with Site 3 could be detected only in 3 quadrats. In Site 3, *Festucetum wagneri* barely resembles the steppe quadrats of the two other sites. This community merges with moss and lichen-rich annual grassland, sometimes with *Festucetum vaginatae*.

The contrast is even more obvious when the three maps are compared based on the calculation of similarities on presence-absence data (Fig. 5). Here – unlike in the former case – not even Site 1 and 2 resemble to each other. At Site 1 coincidence with the traditional vegetation map can only be found in an extreme situation: at the meadow steppe. The borders between open perennial grasslands and *Festucetum wagneri* become blurred owing to the steppe plants that penetrate into the former community. Similarly, at Site 2 systematic coincidence with the units of the traditional map is minimal. At Site 3 – in this species-poor landscape – the floristic difference between *Festucetum wagneri* and moss and lichen-rich annual grassland decreases considerably in some quadrats. This is indicated in the map where the two types merge into each other in some cases, a phenomenon that can be detected also at cover-based similarities.

Degree of steppe quality

To express the richness in steppe plants, a system was elaborated, where all species were evaluated and scored according to their differential affinity to dry grasslands including steppe communities in Hungarian plains (taking into consideration all substrates). The given scores are as follows: Sand steppe specialists: 10; Sand steppe generalists: 9; Sand steppe weeds: 7; Species of the open sand steppes: (*Festucetum wagneri*): 5; Common species of the sand meadows and the sand steppes: 5; Common species of the sand steppe woodlands and the sand steppes: 5; Common species of the open sand grasslands and the sand steppes: 3; Common species of the sand steppe woodlands, the sand meadows and the sand steppes: 3. All other species have the score 0. Summing up the scores for each quadrat, maps of the degree of steppe character are created. According to Fig. 3, at Site 1 all quadrats bear steppe character, strong steppe quadrats dominating. At Site 2, quadrats with various degrees of steppe quality occur in similar proportions, but extremes are also present. At Site 3 strong steppe quadrats are rare and those in which steppe plants are lacking, occur in considerable numbers.

As mentioned above, a differentiation was made among the steppe plants. A group of species bound almost exclusively to the communities belonging to the sociological group *Festucion rupicolae* were distinguished as specialists, while plants having lower affinity to this group were considered to be generalists. According to Fig. 3, Site 1 is the remarkable one among the investigated sites when only specialists are taken into consideration. It is a bit surprising that generalists do not dominate here, but at Site 2. At the same time, Site 3 is equally poor in both respects.

Table 1. Frequencies in the two groups of steppe plants. Note that the value of the possible (maximum) frequency is 98

	Site 1	Site 2	Site 3
SPECIALISTS			
Achillea pannonica	21	1	3
Asperula cynanchica	10	1	10
Bromus inermis	4	13	–
Chamaecytisus ratisbonensis	1	6	–
Helictotrichon pubescens	4	2	–
Hieracium echioides	7	9	–
Linaria angustissima	1	3	–
Stachys recta	4	1	–
Helianthemum ovatum	26	–	1
Anthyllis vulneraria ssp. *vulneraria*	6	–	–
Aster linosyris	66	–	–
Astragalus onobrychis	15	–	–
Campanula sibirica	1	–	–
Chamaecytisus austriacus	13	–	–
Dorycnium herbaceum	10	–	–
Fragaria viridis	1	–	–
Hieracium bauhinii	1	–	–
Jurinea mollis	18	–	–
Medicago falcata	4	–	–
Melampyrum barbatum	2	–	–
Oxytropis pilosa	1	–	–
Pulsatilla pratensis ssp. *nigricans*	1	–	–
Ranunculus polyanthemos	5	–	–
Sanguisorba minor	1	–	–
Scorzonera purpurea	10	–	–
Senecio jacobaea	1	–	–
Thesium linophyllon	2	–	–
Trifolium montanum	1	–	–
Agropyrum intermedium	–	4	–
Allium flavum	–	2	–
Senecio integrifolius	–	4	–
Turritis glabra	–	1	–
Veronica prostrata	–	3	–
Viola hirta	–	1	–
Number of species	28	14	3

Table 1 (continued)

	Site 1	Site 2	Site 3
GENERALISTS			
Eryngium campestre	17	24	19
Euphorbia cyparissias	26	25	12
Falcaria vulgaris	12	24	3
Galium verum	67	59	14
Phleum phleoides	55	48	2
Pimpinella saxifraga	11	10	4
Poa angustifolia	31	64	20
Seseli annuum	24	27	6
Thesium arvense	3	7	3
Dianthus giganteiformis ssp. *pontederae*	19	28	–
Hypericum perforatum	1	12	–
Knautia arvensis	6	4	–
Poa compressa	1	1	–
Taraxacum laevigatum	1	–	5
Tragopogon pratensis ssp. *orientalis*	7	–	2
Pseudolysimachion spicatum	–	46	8
Draba nemorosa	1	–	–
Gypsophila muralis	1	–	–
Petrorhagia saxifraga	1	–	–
Carex praecox	–	33	–
Cruciata pedemontana	–	3	–
Tragopogon dubius	–	1	–
Verbascum lychnitis	–	30	–
Number of species	18	18	12

For details, a comparison of the three sites was accomplished specifying all the steppe specialists and generalists (Table 1).

As many as 19 specialists have an exclusive affinity to Site 1. On the other hand, no species preferring Site 3 could be found. Interestingly and in contrast to specialists, numerous generalists occur with high frequency in all the three sites.

Abiotic factors

One may ask the question whether the climate alone is responsible for these trends? Does the substrate have an effect also? It can be believed that the physical parameters of the substrate show a systematic change in the given direction. Among them the granulation of the sand, more precisely the various ratios of the fine and rough particles may be responsible. As a hypothesis it may be assumed that the dominance of fine particles in the sand, that of the loess and clay fractions

Table 2. Averages, 95% confidence intervals (in parentheses) of the values of the physical fractions at the three sites. (Arcus sinus transformed values were used in the calculations and results retransformed into %)

	Site 1	Site 2	Site 3
Rough sand	45.48 (42.98–47.98)	51.88 (49.90–53.87)	40.67 (38.04–43.32)
Fine sand	45.64 (43.69–47.60)	43.50 (41.47–45.54)	54.33 (51.65–57.00)
Loess	1.58 (1.05–2.21)	0.73 (0.49–1.02)	1.03 (0.72–1.41)
Clay	5.54 (5.05–6.05)	3.07 (2.81–3.34)	2.80 (2.44–3.18)

favor the development of closed steppe grasslands and forests, while a high ratio of rough sand with its low water retention capacity support merely open grasslands.

For this reason physical fractions of the basic parent material were investigated at 49 points in each 2-hectare plot (see Table 2).

The data show that the gradient can not be explained purely on the basis of the quality of the basic parent material.

In spite of this, the investigation of the organic matter content shows different results (Table 3). This parameter, depending strictly on the biological production of the vegetation, is an integrated measure of the site quality in the arid areas. At Site 1, high values predominate, while at Site 2 low and high values as indicators of the site heterogeneity could be observed. At Site 3 slight quantities are characteristic, exceptions are the several quadrats on the place of former meadows.

CONCLUSION

Regarding the community level, a parallel study on the texture and structure of the open perennial grassland (KOVÁCS-LÁNG *et al.* 1999) was carried out along the same gradient. This research revealed that average species richness and canopy cover decreased significantly towards the dry end of the transect. The proportion of perennials in *Festucetum vaginatae* areas decreased as well, whereas proportion of annuals increased with increasing aridity. Classifying the species based on their geographic range, it was found that several species with European and Eurasian distribution occurred mainly or exclusively at the northern "wet end" of the

Table 3. Averages and 95% confidence intervals (in parentheses) of values of soil organic matter content at the three sites. (Arcus sinus transformed values were used in the calculations and retransformed into %)

	Site 1	Site 2	Site 3
Soil organic matter content	4.31 (3.90–4.73)	2.27 (2.00–2.57)	1.44 (1.18–1.73)

transect, while the share of species with continental or sub-Mediterranean distribution was smaller.

Exceeding the community level, the present paper examines the effect of the spatial climatic changes mainly at the level of landscape. Analyzing traditional vegetation maps of the three sites that are situated along the gradient, we showed that semidesert-like communities became dominant with the increasing aridity. Simultaneously, the closed grasslands were modified considerably as well. So *Festucetum wagneri* "lost" almost all of its steppe characteristics in the most arid landscape (Site 3) undergoing a transformation along the transect, which demonstrated its considerable plasticity in floristic composition. This – and similar phenomena – are the causes why the vegetation maps based on calculated similarities are different from those which where created on a traditional way.

The species pool of the landscapes – being isolated from one another – is different, which is an other reason why some communities show segregation (despite their common dominant species) according to the landscapes.

As an ultimate factor, soil organic matter content changes in relation to precipitation. So the question whether the effect of the macroclimate expresses itself in the flora and in the composition of the vegetation has been positively answered.

Attention has to be paid to another issue concerning the structure of the Pannonian forest steppe. At the beginning of this paper reference was made to previous results regarding the general decrease of forest plants from north to south in the Duna-Tisza Interfluve. In accordance with this finding, it was hypothesized that distributional maps of plants characteristic of closed steppe grasslands will yield point clouds that show a trend of increase in an opposite direction compared with that of the forest species. This expectation can be reasoned by the transitional character of this zone best recognizable in the wide Eastern-European space, where this zone (or biome) is influenced both by the belt of closed forests from the north and by the steppe belt from the south. However, data in Table 1 do not support this expectation.

Maybe the situation in the Carpathian Basin is not as clear as in Eastern Europe due to its closed space, where the position of the zones is somewhat concentric. For solving the contradiction and for correct interpretation of the structure of forest steppe, the preparation and the evaluation of further intersections are needed involving loess substrates as well.

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