VEGETATION-ENVIRONMENT RELATIONSHIPS IN DRY CALCAREOUS GRASSLAND

MONIKA JANIŠOVÁ

Institute of Botany, Slovak Academy of Sciences, Dúbravská cesta 14, 845 23 Bratislava, The Slovak Republic, e-mail: monika.janisova@savba.sk

Abstract

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Relationships between dry grassland vegetation and environmental factors were investigated at a small scale. Dry calcareous grasslands of *Festucetalia valesiacae* were studied in Považský Inovec Mts. (western Slovakia). Species frequency data were collected on a transect located in south-north direction across the ridge so that the vegetation of southern slope, the top plateau and northern slope was involved. Nine environmental factors were measured in basic sample units including topographic, pedological and biological characteristics. Three main environmental factors were found to be responsible for differenciation of the studied vegetation types, intensity of solar irradiation playing the crucial role among them. The second most important factor was soil depth, and the slope had also a significant effect. The complex environmental factor indicated as xericity can be characterised as a gradient of increasing solar irradiation, pH, and soil skeleton content and decreasing content of both humus and fine soil particles. In analysis of the southern slope after excluding the role of aspect data set variation was explained mostly by soil properties: soil depth, humus content and pH. On the northern slope the most important factors were solar irradiation followed by soil depth. The effect of environmental variables upon cryptogams and phanerogams seems to be different. As expected, the vascular plants were controlled by the same factors that were confirmed to be relevant for the whole species set: solar irradiation, soil depth and slope. In cryptogams, solar irradiation plays obviously a minor role and soil properties together with the vegetation cover seem to be the limiting factors affecting their distribution.

Key words: Festucetalia valesiacae; Detrended Correspondence Analysis; Canonical Correspondence Analysis; Xericity; Frequency data; Coenocline; western Slovakia

Abbreviatons: DCA = Detrended Correspondence Analysis; CCA = Canonical Correspondence Analysis; *Poo-Festucetum* = *Poo badensis-Festucetum pallentis* Klika 1931 corr. Zolyomi 1966; *Festuco-Caricetum* = *Festuco pallentis-Caricetum humilis* Sillinger 1930 corr. Gutermann et Mucina 1993; *Carici-Seslerietum* = *Carici humilis-Seslerietum calcariae* Sillinger 1930.

Nomenclature: Marhold, Hindák (1998)

Introduction

Dry grassland communities of the *Festuco-Brometea* reflect sensitively differences in the environmental conditions of habitat even at the minor scale (Mucina, Kolbek, 1993; Sillinger, 1931; Maglocký, 1978, 1979; Rychnovská, Úlehlová, 1966; Pivničková, 1973; Slavíková, 1983). Dry grasslands of Považský Inovec Mts. are subject of phytosociological and ecological studies yet since the beginning of this century (Sillinger, 1931; Maglocký, 1973, 1978, 1979; Mucina, Bartha, 1999). A significant gradient in vegetation composition corresponding with a complex environmental gradient was revealed in the top parts of ridges running in the north-south direction. The distinct vegetation types (by phytocoenologists classified as different associations) distributed at the southern slope, the plateau and the northern slope, are sharply separated topographically as well as ecologically. The complex environmental gradient (let us call it xericity) is determined by the joint influence of numerous partial factors which can be measured.

Over the last decades several studies were devoted to investigation of vegetation-environment relationships in dry grasslands at a large scale (Thompson et al., 1996; Ejrnćs, Bruun, 2000; Duckworth, et al., 2000). In this study relationships between dry grassland vegetation and environmental factors were investigated at a micro scale. The basic idea was to assess the effect of hypothetical main environmental gradient and to determine the partial factors (topographical, pedological or biological) by which it is supported. Further aims were to assess the relative importance of individual environmental factors upon the vegetation, to compare their role in different community types and their influence upon cryptogams and phanerogams.

Materials and methods

Study site

The study site is located in the Považský Inovec Mts (western Slovakia), near the village Lúka nad Váhom (latitude 48° 39c 252 N, longitude 17° 54c 202 E). The studied communities were sampled at an altitude of 380–390 m. At the location, the Triassic dolomite supports shallow protorendzina soils. The whole area has a warm climate with mean annual temperature 9.2°C, mean temperature of the warmest month (July) 19.3°C and the mean annual precipitation 625 mm at the nearby located climatic station Piešťany. The microclimatic conditions of grasslands in the region were studied in Maglocký (1978).

Phytosociologically, the studied communities belong to the class *Festuco-Brometea* B r-B l. et R.T x. 1943, order *Festucetalia valesiacae* B r-B l. et R.T x. 1943 and to three associations: *Carici humilis-Seslerietum calcariae* S i l l i n g e r 1930, *Festuco pallentis-Caricetum humilis*

S i l l i n g e r 1930 corr. G u t e r m a n n et M u c i n a 1993 and *Poo badensis-Festucetum pallentis* K l i k a 1931 corr. Z o l y o m i 1966. The detailed phytosociological description of the dry grassland vegetation in the region is given by Sillinger (1931) and Maglocký (1979) and the syntaxa characteristics are given also by Mucina, Kolbek (1993).

Vegetation sampling

The data were collected on a transect located in south-north direction across the ridge so that the vegetation of southern slope, the top plateau and the northern slope was involved. This was aimed to comprise the hypothetically dominant environmental gradient – the xericity. Transect was composed of 50 adjacent quadrats (basic sample units) with size 50 by 50 cm, each divided into 25 microquadrats with size 10 by 10 cm. The rooted frequency of all species was recorded in microquadrats. Sampling was performed in May–June 1993. As the studied grassland vegetation varies significantly during the growing season, some of the spring terophytes and later summer herbs (e.g. *Anthericum ramosum*) could be underestimated.

Environmental variables

Environmental factors were measured in basic sample units. Their characteristics together with the methods used for their measurment are shown in Table 1. Even though slope and PDSI are not independent both were used as explanatory variables. Their correlation was very poor (Table 2) and they were thought to express different effects upon the vegetation. Soil analyses were done following methods of Hraško (1962).

Data analysis

The association between environmental variables was expressed by Spearman rank correlation coefficient (Table 2) as most variables had not the normal distribution. Bonferroni correction for multiple comparison methods was used. The significance level for the whole test was determined as the type I error probability in at least one partial test: a_d=2P/[s(s+1)]. The vegetation cover was used as an explanatory variable (biological factor reflecting the space saturation by plants) only in the analysis of cryptogams.

T a b l e 1. Environmental factors and their characteristics

No.	Code	Environmental factor	Type of factor	Unit	Range	Comments
1	slope	slope	topographic	[°]	0–28.2	measured by a compass (90° scale)
2	PDSI	potential direct solar radiation	topographically dependent	[kJ]	52.7–75.2	estimated according to Jeník, Rejmánek (1969) using the values of aspect and slope
3	soil depth	depth of soil	topographically dependent	[cm]	1.95–13.75	measured by a pin with diameter 2.5 mm (down to reaching the bedrock). The average value was computed out of ten measurements in each basic sample unit
4	SDH	heterogeneity of soil depth	topographically dependent		0.95–5.34	standard deviation from average computed out of ten measurements of soil depth
5	pH	pH/KCl of soil	soil chemical		6.74–7.35	measured in the upper soil layer (up to the depth 10–15 cm)
6	< 0.002	% of soil particles < 0.002 mm	soil physical	[%]	2.46–9.51	as *pH*
7	0.1–2.0	% of soil particles 0.1–2.0 mm	soil physical	[%]	25.36–61.55	as *pH*
8	humus	soil humus content	biologically dependent	[%]	4.57–19.73	calculated out of the overall carbon content
9	cover	vegetation cover	biological	[%]	0–97	percentage cover of both cryptogams and phanerogams

T a b l e 2. Spearman rank correlation between environmental factors

Environmental factor	Slope	PDSI	Soil depth	SDH	pH	<0.002	0.1–2.0	Humus	Cover
Slope	–								
PDSI	0.094	–							
Soil depth	– 0.173	– 0.503*	–						
SDH	0.032	– 0.215	0.617***	–					
pH	0.093	0.709***	– 0.385	– 0.058	–				
<0.002	– 0.001	– 0.749***	0.381	0.109	– 0.774***	–			
0.1–2.0	0.486*	0.349	– 0.682***	– 0.398	0.219	– 0.325	–		
Humus	– 0.228	– 0.784***	0.417	0.013	– 0.826***	0.824***	– 0.256	–	
Cover	0.003	– 0.823***	0.599***	0.294	– 0.772***	0.759***	– 0.272	0.753***	–

*** – coefficients significant at $\alpha = 0.001$, * – coefficients significant at $\alpha = 0.05$

For the gradient analysis the computer program CANOCO version 3.12 (ter Braak, 1987, 1990) was used. In most analyses (except the analyses of phanerogams and cryptogams) rare species with the frequency less than 1/5 the frequency of the most frequent species were downweighted in proportion to their frequency according to Hill (1979). Moss species were made passive by giving them a negligible weight 0.01 in all analyses except the one analysing the cryptogams – environment relation.

Nine explanatory variables were used (Table 1). As the basic sample units were contiguous quadrats in line transect, individual quadrats are related to their neighbours at both sides. Thus the results may depend on the quadrat size or their relation to the community structure. Therefore, a parallel spatial pattern analysis was performed (Janišová, unpubl.). In Monte Carlo permutation test the problem of autocorrelation was partially avoided by using appropriate restricted permutation for line transects.

An indirect gradient analysis – the Detrended Correspondence Analysis (DCA, Hill, 1979) – was applied for preliminary analysis of species data. Detrending was done according to the CANOCO propositions (ter Braak, 1987, 1990). For a constrained ordination the CCA or RDA were used according to the gradient length estimated previously by the DCA. The method of forward selection was used to find out a minimal set of variables that explain the species data. Only statistically significant (at the 5%-level) environmental factors tested by the Monte Carlo permutation test were used in analyses (ter Braak, 1990). Altogether 999 restricted permutation were used to test the selected variable.

The percentage variability of species data explained by individual environmental factors was determined by the CCA and the RDA respectively, while the factors were used in turn as the only environmental variables. Then the variability explained by the individual variable is the ratio of the eigenvalue of the first axis in direct ordination and the total variation of both species and samples matrices (Řkland, Eilertsen, 1994).

The vegetation types were distinguished by the cluster analysis using the program NCLAS (Podani, 1988). Results are used in Fig. 3 and Table 3 and notation of clusters by letters A to D for distinct vegetation types is used throughout the text, tables and figures. The ß-flexible clustering method (ß = -0.25) with resemblance matrix according to the Wishart's Similarity Ratio, was used for numerical classification. Four degrees of frequency were used as quantitative characteristics of species in basic sample units: 1 – present in 1–5% of microquadrats, 2 – present in 5–25% microquadrats, 3 – present in 25–50% microquadrats, 4 – present in 50–100% microquadrats. (Table 3).

As the transect comprised several floristically and ecologically distinct vegetation types, the influence of environmental factors was analysed in each type separately. Similarly, the influence of environmental variables was analysed on both the southern and the northern slopes.

To compare the influence of environmental factors upon the phanerogams and cryptogams species data were divided into two sets that were analysed separately by the direct gradient analysis as described above. All species that did not belong to the analysed set were made passive by assigning them the weight 0.01.

T a b l e 3. Species frequency in basic sample units. Quadrats (columns) are ordered according to the result of cluster analysis. Frequency categories: present in 1 - 1–5%, 2 - 5–25%, 3 - 25–50%, 4 - 50–100% microquadrats

Cluster	B	A	C	D
Quadrat number	1111121111 68795043215	1 142368097	223222322223333 180279135645423	333344444444544 678912304789056
Sedum album	122--21----	---------	---------------	---------------
Erophila verna	1-----1----	---------	---------------	---------------
Cerastium pumilum	12----1----	---------	---------------	--------------1
Fulgensia fulgens	33442221---	---------	---------------	---------------
Poa bulbosa	32112-21222	------1--	---------------	---------------
*Jovibarba * glabrescens*	22211------	---11----	---------------	---------------
*Dianthus * lumnitzeri*	-212221-1--	---------	2--------------	---------------
Catapyrenium sp.& *Psora* sp.	44443321122	12-------	--1--2-1-----32	1----2---------
Draba lasiocarpa	3333332322-	----31-1-	---------------	---------------
Silene otites	1------1---	--1------	---------------	---------------
Alyssum montanum	1233222112-	-2--22211	-----1---------	---------------
Thymus praecox	43333244333	344344442	-----12-21-----	2-11-22--1-12--
Potentilla arenaria	313213222--	-----1121	322111--2221121	-----22--1-----
Linum tenuifolium	12312222-22	-112-2221	---22112---1-2-	1---------11---
Fumana procumbens	33233343432	221321323	3332322-22---22	1--------------
Ditrichum sp.& *Bryum* sp.	344434221-2	21-22---3	------3----2244	---------------
Stipa eriocaulis	--121222322	23-123113	2222222232---12	--------112121-
*Helianthemum * obscurum*	-----1--113	122212231	--12221-2-22233	2222344233222-1
Teucrium montanum	-1---223222	324323333	123223342333333	333333222-1221-
Carex humilis	---2-2-3122	234344344	444444444444433	444444434444444
Tithymalus cyparissias	1---1--1---	222222222	----122-22112--	1---1-1---112--
Biscutella laevigata	-----------	-2111--1-	-----12------1-	----------22212
Thesium alpinum & linophylon	21---------	---------	211322233233122	3222-2-2-22-222
Bupleurum falcatum	-----------	---------	---2111-2212---	2322222-2222211
Trinia glauca	---------1-	---------	1----1-2-2112-2	-2222213-------
Scorzonera austriaca	--1-2------	---------	1--2-112--21---	---------------
Sesleria albicans	-----------	---------	-----------22--	2222-22-4333344
Genista pilosa	--------1--	---------	--------2-21---	33213-2-2344443
Anthericum ramosum	-----------	---------	---------------	123222232221222
Festuca rupicola	-----------	---------	---------------	-122-23--------
Cuscuta epithymum	-----------	---------	---------------	-1-21--3-11----
Allium senescens	-----------	---------	---------------	-1122----------
Acinos alpinus	-----------	---------	---------------	1--1-2---------
Campanula moravica	-----------	---------	-------------1-	----2-2--22--22
Phyteuma orbiculare	------1----	---------	1--------------	---------2-2311
Vincetoxicum hirundinaria	-----------	--1-1--1-	-----------1---	--1---1-2--1-2-
Festuca pallens	34444443443	334322222	344333443232344	333444231332212
Tortella sp.& *Hypnum* sp.	44434444444	322233431	344443344444432	444444444434344
Sanguisorba minor	11-22221113	233332222	211222233333222	2222222222222-1
Globularia punctata	1-22-232222	1-2223222	223332334433333	-2222222-2-----
Leontodon incanus	2---12211-2	22-21222-	1111222--121-1-	3232122222322-2
Cladonia cf. *furcata*	24334333222	1--------	233234433321344	2-111--2----1--
Asperula cynanchica	2--21-12-1-	3222222--	-------122--211	-2--------2-2--
Seseli hippomarathrum	-1-----1--1	22-----2-	--------------2	---------1-1---
Pilosella officinarum	-1--------1	-2-2-2---	---------------	12--1-1-1-121--
Campanula sibirica	-----------	1--------	-21------------	---1-----------
Scabiosa ochroleuca	------2----	--1-----1	--1-----3-2111-	1---1-1--------
Anthyllis vulneraria	-----1-----	-1-------	---------------	122------------
Inula ensifolia	-----------	---1----1	---------------	---1-----1---1-
Arenaria serpyllifolia	122--------	---------	----12---------	---------------
Pilosella bauhinii	-----------	2-22-----	---------------	----------1----
Allium flavum	-1---------	-------1-	---------------	-----------2---

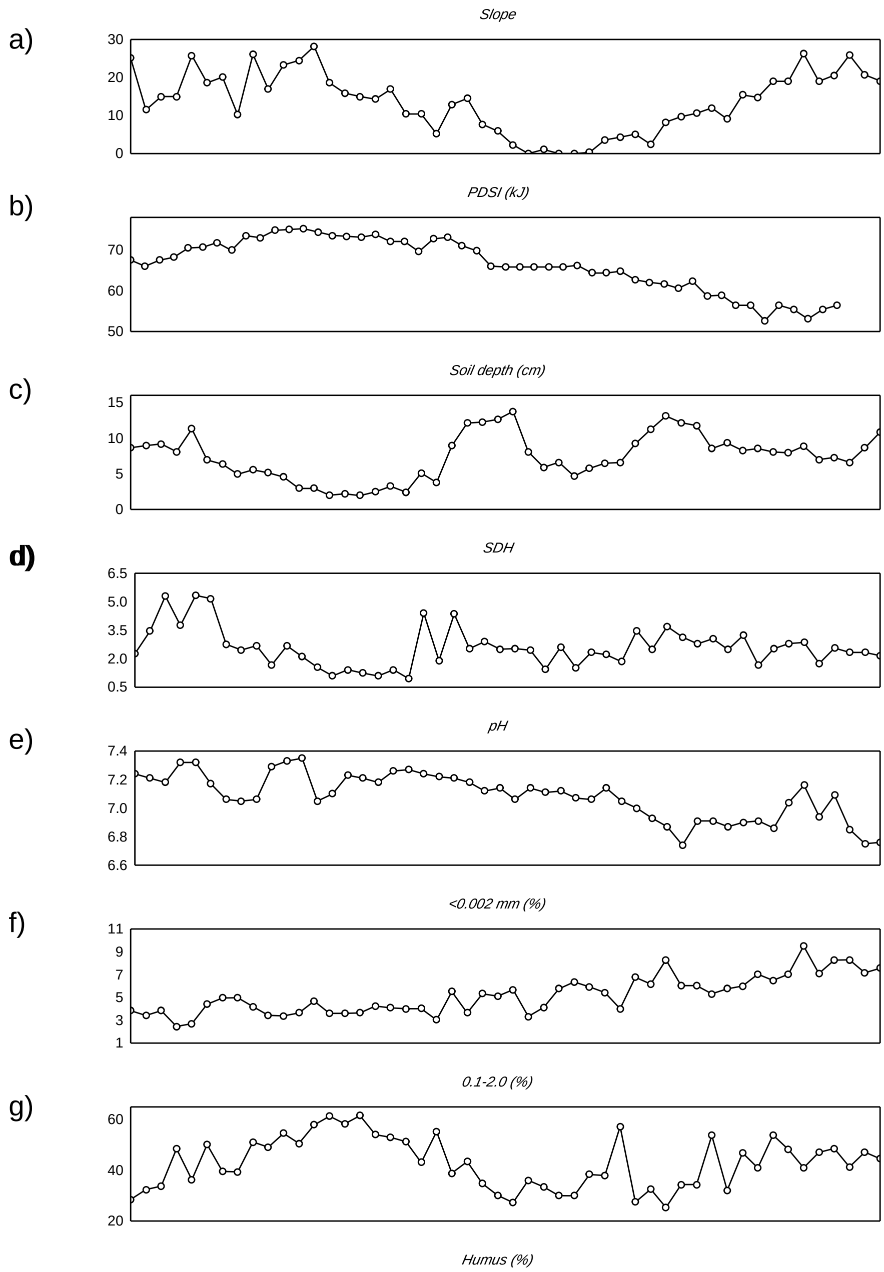
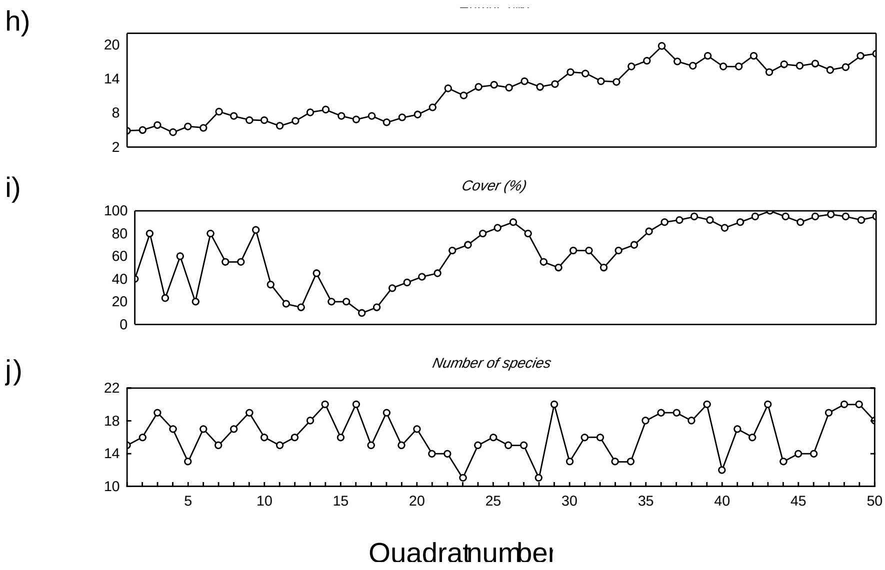


Fig. 1. Values of environmental factors measured along the transect and number of species in basic sample units: a) slope, b) potential direct solar irradiation, c) depth of soil, d) standard deviation of soil depth, e) pH, f) proportion of soil particles smaller than 0.002 mm in diameter, g) proportion of soil particles from 0.1 to 0.002 mm in diameter, h) soil humus content, i) cover of vegetation, j) species number of vascular plants.



Results

Environmental factors

The values of the measured environmental variables vary rather strongly along the transect (Fig. 1a-i). The correlation between environmental factors is revealed in Table 2. Highest correlation coefficients were found between *humus* and both *pH* (negative) and *< 0.002* (positive). *PDSI* showed significant negative correlation with *cover*, *humus*, *< 0.002* and *soil depth*, positively was significantly correlated only with *pH*. Vegetation cover was strongly negatively correlated with *PDSI* and *pH*, positively was correlated with *< 0.002*, *humus* and *soil depth*. The least correlated variables were *slope* and *SDH*.

Vegetation analysis

According to the cluster analysis four groups of quadrats may be distinguished. They represent floristically and ecologically distinct types of vegetation (Table 3).

Cluster A (quadrats 1, 2, 3, 4, 6, 7, 8, 9 and 10): Vegetation of this type is typical of steep southern slopes, to some extent protected against the direct irradiation by both steep slopes and low oak group in the vicinity. Together with the dominant xerophilous species (*Carex humilis*, *Stipa eriocaulis, Alyssum montanum, Fumana procumbens, Thymus praecox*) also several less xerophilous species common on the northern slopes are present

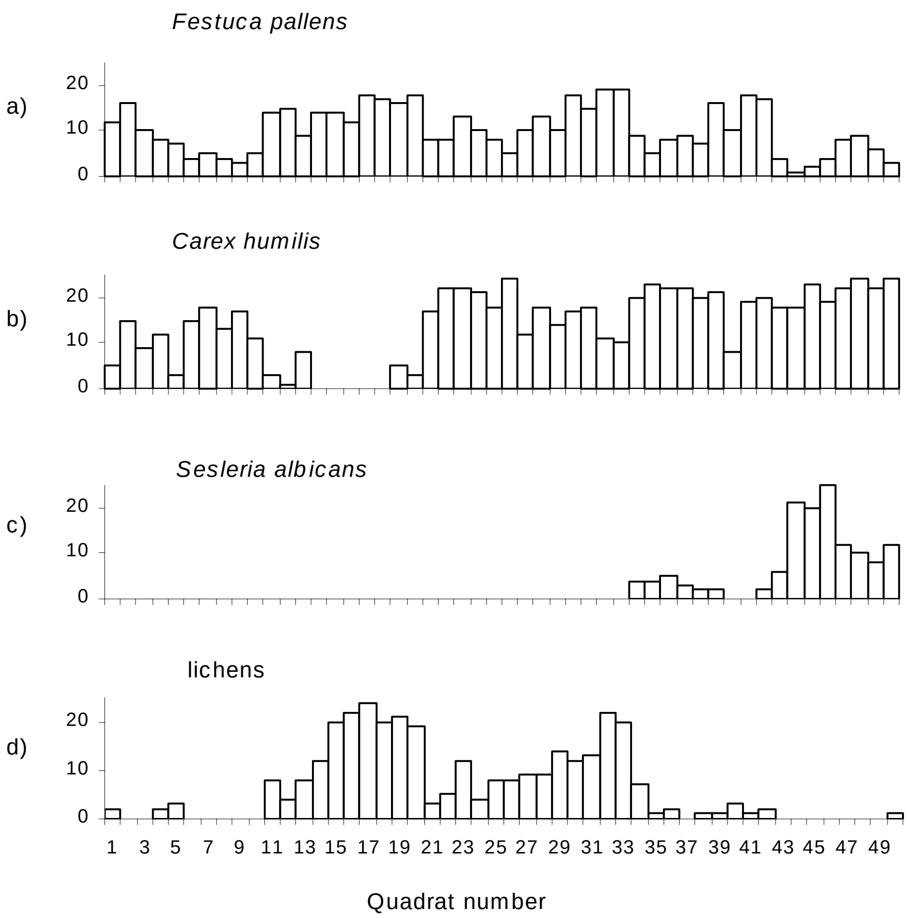


Fig. 2. Frequency of dominant grasses and lichens in basic sample units. Number of microquadrats with species presence is given (maximum frequency is 25) for a) *Festuca pallens*, b) *Carex humilis*, c) *Sesleria albicans*, d) lichens (all species present).

(*Vincetoxicum hirundinaria, Pilosella officinarum, Biscutella laevigata*). Syntaxonomically, the stands best correspond to the *Festuco pallentis-Caricetum humilis*.

Cluster B (quadrats 5, 11, 12, 13, 14, 15, 16, 17, 18, 19 and 20): This type of vegetation occurs on the driest edges of southern slopes intensively exposed to the solar irradiation. Floristically it is differentiated by the presence of most xerophilous species such as *Sedum album, Jovibarba * glabrescens, Dianthus * lumnitzeri, Poa bulbosa, Draba lasiocarpa* and *Fulgensia fulgens* as well as low abundance of strongly competitive but less drought tolerant species e.g. *Carex humilis* (Fig. 2b) and *Teucrium montanum*. Typical features are the low vegetation cover (Fig. 1i) and rocky skeletal soil exposed to the erosion. Syntaxonomically, it belongs to the *Poo badensis-Festucetum pallentis*.

Cluster C (quadrats 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34 and 35): Quadrats sampled on the top plateau and upper parts of northern slope. The vegetation is almost closed, significantly structured according to the dominant tussocks of *Carex humilis*. Species such as *Globularia punctata*, *Scorzonera austriaca, Bupleurum falcatum, Potentilla arenaria* and *Thesium linophyllon* have their optimum here. It represents a typical example of the *Festuco pallentis-Caricetum humilis*.

Cluster D (quadrats 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49 and 50): This type of vegetation is distributed on steeper northern slopes protected from strong direct irradiation. The closed stands are dominated by *Sesleria albicans* (Fig. 2c) and from the former vegetation types are differentiated by the occurrence of *Genista pilosa, Anthericum ramosum, Campanula moravica, Festuca rupicola*, etc. (Table 3). Syntaxonomically it belongs to the *Carici humilis-Seslerietum calcariae*.

DCA

As the DCA is an unconstrained ordination, the analysis was performed on the species data alone. Subsequently, an environmental interpretation was made by superimposing environmental data on the ordination plot and looking for patterns and correlation. The results are shown in Fig. 3 and Table 4. Among the environmental variables *PDSI* has the highest correlation with the first ordination axis. High correlation emerged also between the first axis and both *humus* and *< 0.002* which are negatively correlated with *PDSI* (Table 2). Taken together, the complex environmental gradient controlling the floristic composition of vegetation is the xericity, best interpreted by potential direct solar irradiation that decreases along the first axis. On the other hand content of both humus and fine soil particles increase along this axis.

The vegetation is clearly differentiated along the first axis while the second axis explains much less variance of species data (Table 4). The second axis showed the highest correlation with *slope*.

As follows from Fig. 3 the transition between the *Festuco-Caricetum* and the *Carici-Seslerietum* is rather continuous (they overlap to some extent at the ordination plot). On the other hand there is a clear isolation of the *Poo-Festucetum* from the rest of quadrats that suggests sharp boundaries in a mosaic of plant communities on the southern slope. Nevertheless, the three different associations emerge clearly in three separate parts along the first axis. So do the species typical of the individual communities. Species of the *Poo-Festucetum* including the lichens and spring ephemeral plants are most abundant in the left part of the diagram with high solar irradiation and shallow humus poor soil. Species with distribution culminating in the *Carici-Seslerietum* occur in the right part of the diagram in least xeric habitats with deep fine soil. Species of the *Festuco-Caricetum* and species common in all three vegetation types are distributed between the two extremes in the middle of the plot (Fig. 3).

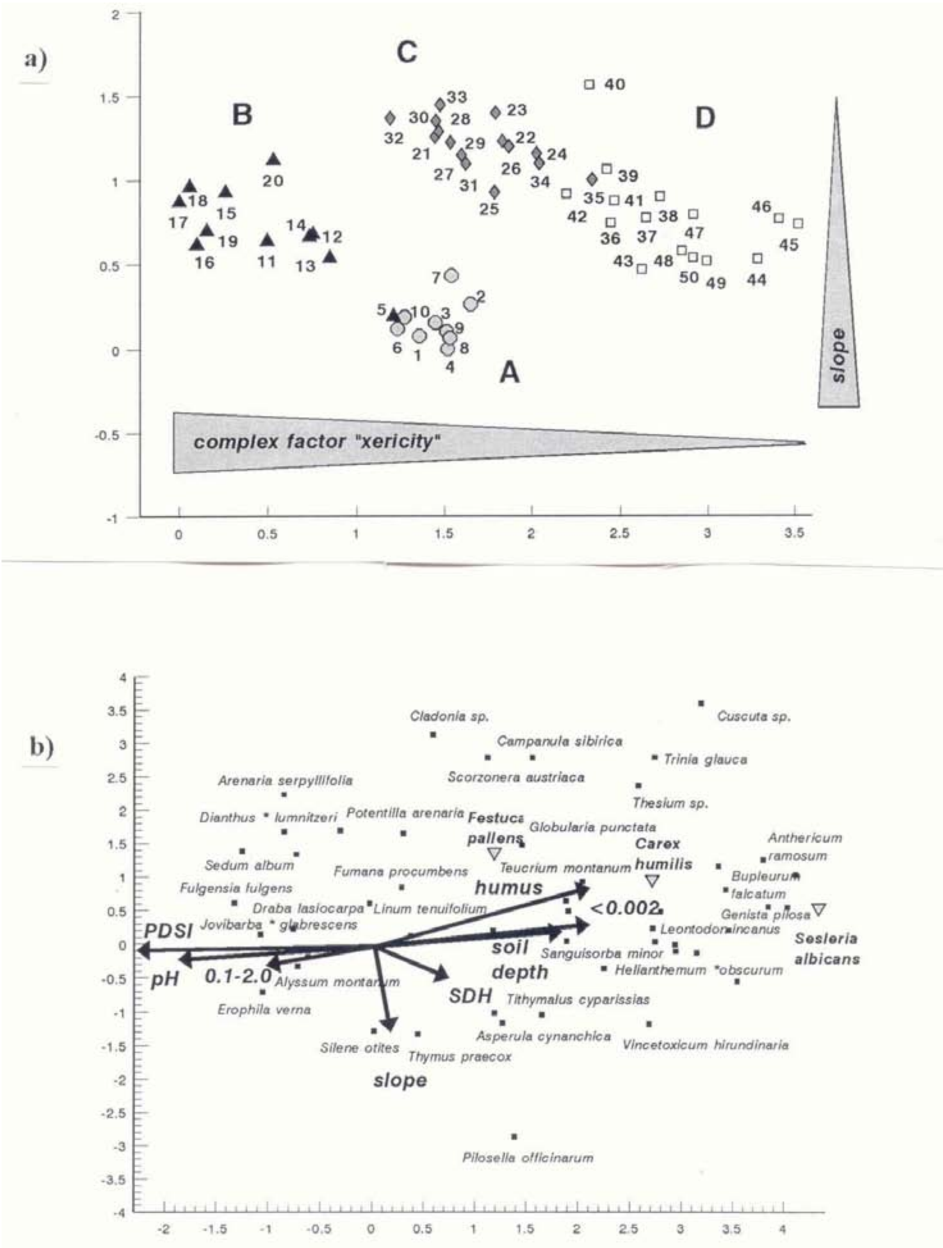


Fig. 3. Detrended correspondence analysis a) ordination diagram of samples, b) ordination diagram of species. Correlation of environmental factors with ordination axes is shown. The position of species dominating different vegetation types is emphasises by triangles.

CCA

T a b l e 4. Detrended correspondence analysis, correlation of species ordination axes with environmental factors, eigenvalues and percentage variances explained

Environmental. factor	Axis I	Axis II
Slope	0.06	–0.64
PDSI	–0.87	–0.04
Soil depth	0.68	0.10
SDH	0.28	–0.25
pH	–0.71	–0.10
< 0.002	0.77	0.14
0.1–2.0	–0.39	–0.17
Humus	0.78	0.45
Eigenvalue	0.49	0.13
% variance explained	29.20	7.90

The CCA uses both species and environmental data in the actual ordination process. The resulting ordination diagram thus expresses not only patterns of variation in floristic composition but also demonstrates the principal relationships between the species and each of the environmental variables. The results of the CCA applied on transect data are shown in Fig. 4, Tables 5 and 6. The analysis supported the assumption on the dominant influence of *PDSI* (responsible for 23% of data set variation). Further significant factors that passed the forward selection were *soil depth* and *slope*. Altogether the three significant factors explained 38% of variation in the data set.

Several environmental variables explain higher percentage of data set variation if they are analysed separately as the only constraining variables. The highest values were found in *PDSI* , *humus* and *< 0.002* (Table 5). In the forward selection only statistically most significant variables are selected. As a consequence, in factors which correlate with them, the proportion on explaining the residual variation is reduced. This is the reason why only three environmental variables have passed the forward selection.

Effects of environmental factors in different vegetation types (RDA, CCA)

Within the *Poo-Festucetum* represented by quadrats of cluster B *slope* was the most important factor explaining 39% of data variation (Table 7). The only significant factor passing the forward selection in cluster A analysis was *0.1-2.0* (explaining 24% of variation) that expresses a physical soil property in terms of soil skeleton content. The vegetation of the top plateau (the *Festuco-Caricetum*, cluster C) was differentiated mostly by differences in *soil depth* responsible for 20% of data variation. In cluster D (the *Carici-Seslerietum*) the *PDSI* passed as the most relevant environmental variable explaining 22% of data variation.

On the southern slope the vegetation was found to be differentiated by three significant factors (Table 7) – *soil depth*, *humus* and *pH* – explaining together 42% of data variation. Ordination plots of the CCA for both species and samples and their relation to the significant environmental variables are depicted in Fig. 5. In the northern slope analysis two

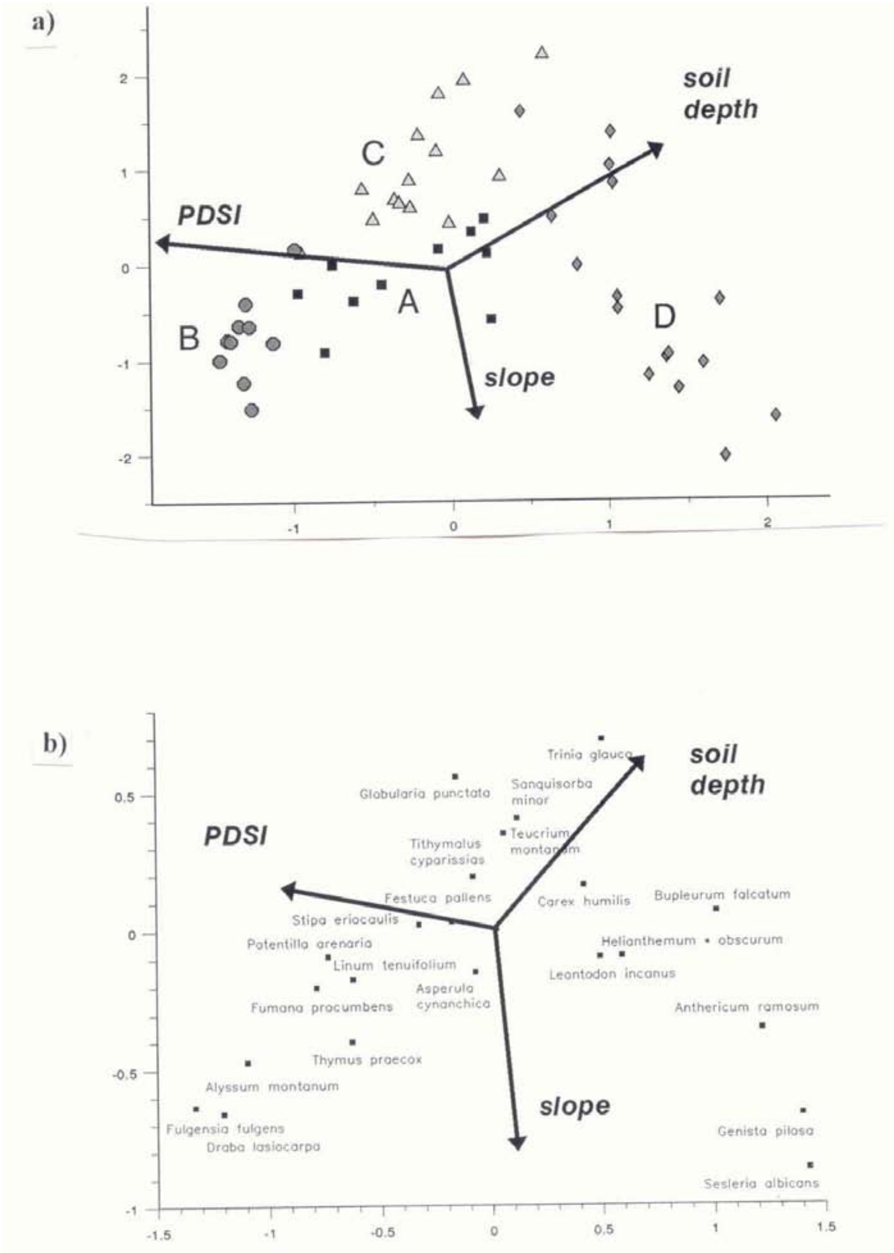


Fig. 4. Canonical correspondence analysis a) samples/environment biplot, b) species/environment biplot. Only environmental factors passed by forward selection and species with higher weight are depicted. The vegetation types marked by different symbols and letters A, B, C and D are described in text.

T a b l e 5. Canonical correspondence analysis, correlation of species ordination axes with environmental factors, eigenvalues and percentage variances explained

Environmental. factor	Axis I	Axis II
Slope	0.08	0.61
PDSI	–0.89	–0.14
Soil depth	0.65	–0.50
SDH	0.25	–0.25
pH	–0.72	0.08
< 0.002	0.79	0.15
0.1–2.0	–0.36	0.56
Humus	0.80	–0.16
Eigenvalue	0.44	0.16
% variance explained	26.40	9.70

T a b l e 6. Canonical correspondence analysis. Test of significance of explanatory environmental variables in different subsets (All species, Vascular plants, Mosses & Lichens). Variation explained – eigenvalue of constrained axis (one constraining variable) divided by the sum of all eigenvalues (total inertia of data set in question). TVE – total variation explained by significant factors (TVE by significant variables) or by all factors analysed (TVE by all variables). Increase of variation explained by inclusion of a variable in forward selection ($P \leq 0.05$) is given in parentheses

No.	Env. factor	Variation explained		
		All species	Vascular plants	Mosses & Lichens
1	Slope	0.07 (**0.06**)	0.07 (**0.05**)	0.06 (**0.08**)
2	PDSI	0.23 (**0.23**)	0.24 (**0.24**)	0.14
3	Soil depth	0.16 (**0.09**)	0.15 (**0.08**)	0.17 (**0.17**)
4	SDH	0.05	0.03	0.09
5	pH	0.16	0.16	0.12
6	< 0.002	0.19	0.19	0.11
7	0.1–2.0	0.09	0.08	0.07
8	Humus	0.20	0.21	0.13
TVE by significant variables		0.38	0.37	0.25
TVE by all variables		0.50	0.48	0.43
Total inertia		1.674	1.599	1.000

factors have passed the forward selection – *PDSI* and *soil depth* – responsible together for 36% of data set variation (Table 7).

T a b l e 7. Canonical correspondence analysis. Test of significance of explanatory environmental variables in different subsets (vegetation types represented by clusters A, B, C and D, vegetation on the southern slope, vegetation on the northern slope). For further explanation see

		Variance explained					
No.	Env. factor	A	B	C	D	S-slope	N-slope
	quadrats	1-4, 6-10	5, 11-20	21-35	36-50	1-25	26-50
1	Slope	0.08	0.39 (**0.39**)	0.08	0.22	0.08	0.27
2	PDSI	0.22	0.08	0.08	0.22 (**0.22**)	0.13	0.28 (**0.28**)
3	Soil depth	0.21	0.20	0.20 (**0.20**)	0.08	0.23 (**0.23**)	0.10 (**0.08**)
4	SDH	0.07	0.20	0.10	0.07	0.12	0.06
5	pH	0.14	0.06	0.08	0.09	0.05 (**0.06**)	0.13
6	< 0.002	0.13	0.15	0.07	0.19	0.07	0.20
7	0.1–2.0	0.24 (**0.24**)	0.11	0.07	0.07	0.18	0.06
8	Humus	0.19	0.09	0.08	0.06	0.16 (**0.13**)	0.16
TVE by sign. var.		0.24	0.39	0.20	0.22	0.42	0.36
TVE by all var.		1.00	1.00	0.67	0.65	0.59	0.57
Total inertia		1.000	1.000	0.601	0.861	1.139	1.115

Effects of environmental factors upon cryptogams and phanerogams

According to the CCA the *PDSI*, *soil depth* and *slope* are the most important environmental factors for vascular plants explaining together 37% of data variation (Table 6). On the other hand, for the cryptogams only two of them are relevant – *soil depth* and *slope.* In the analysis with included *cover* as explanatory variable four factors passed the forward selection (ordered according to their importance): *cover*, *humus*, *slope* and *0.1–2.0* (Table 6).

Discussion

In dry grasslands climatic and soil conditions are along with human influence concerned to be the most important factors affecting their floristic composition (Ellenberg, 1986). Most of dry grassland communities inhabit slopes and plateau that differ in local climatic conditions from the regional climate. The differences in microclimatic conditions were used by several authors to explain the small scale vegetation mosaic of dry grasslands (e.g. Sillinger, 1931; Rychnovská, Úlehlová, 1966; Maglocký, 1978; Slavíková, 1983). According to Maglocký (1979) the vegetation mosaic is a consequence of significant differences in ecological conditions at a small scale while the zonation is more pronounced over dolomites than over limestone. Environmental variables measured at a micro-scale were used also in this work. The results have shown that the influence of dominant environmen-

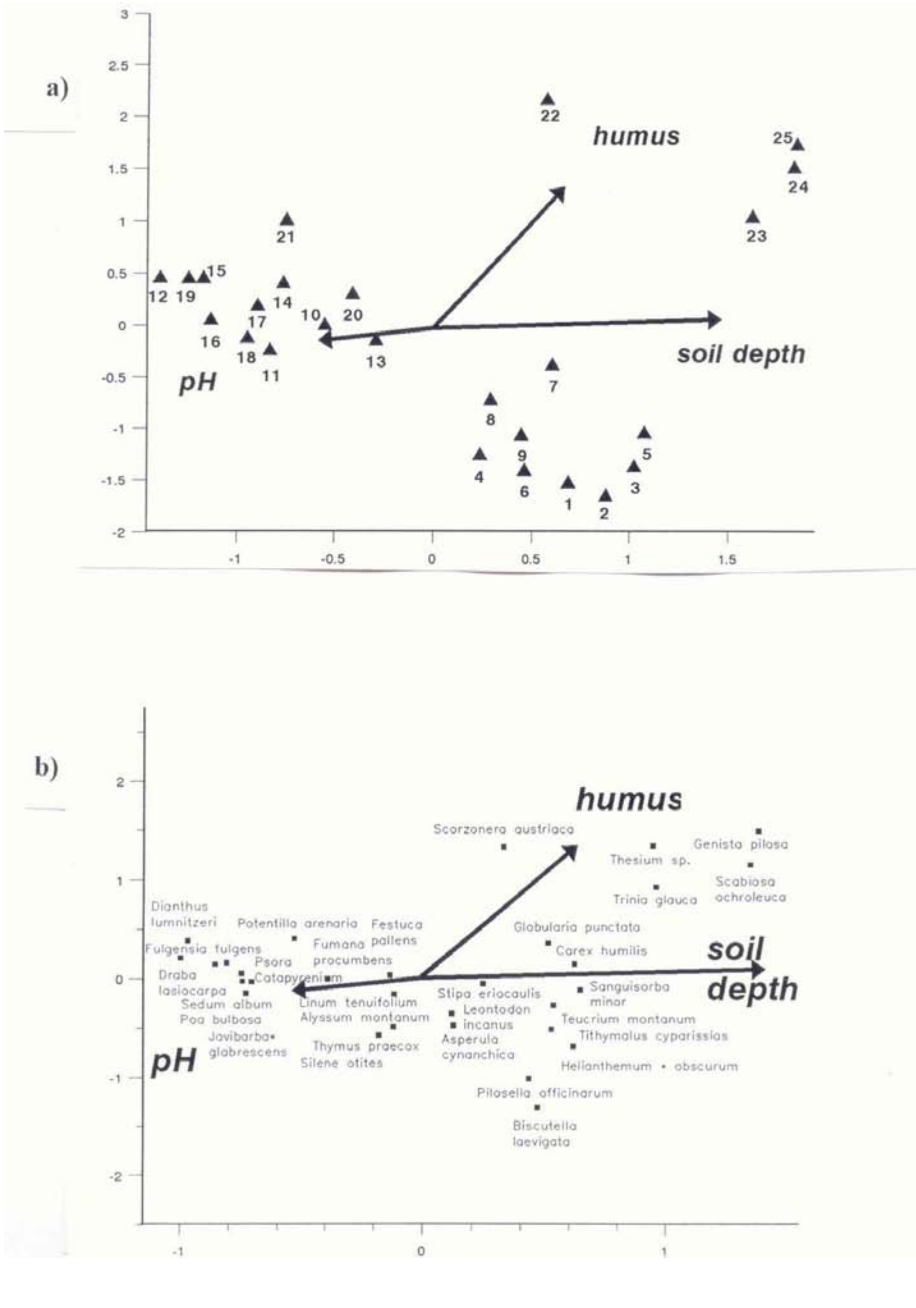


Fig. 5. Canonical correspondence analysis of the southern slope (samples 1–25). a) samples/environment biplot, b) species/environment biplot.

tal factors is visible yet at the level of decimetres and it is reflected sensitively in changes of vegetation composition.

As follows from the results the vegetation of the studied dry grasslands is differentiated by three main environmental factors, intensity of solar irradiation playing the crucial role among them. The second most important factor is the soil depth, and the slope has also a significant effect. All these factors are either topographically dependent (*PDSI* is determined by location and relief form, *soil depth* depends on relief in combination with biological factors) or directly topographical (*slope*). It suggests these to be the primary factors determining finely the variation of both pedological and biological conditions with a secondary effect upon the vegetation. E.g. on sites with high solar irradiation on steep slopes the vegetation cover is low, so is the standing crop and subsequently the humus formation. In the analysis of individual factors *humus* had the second highest value of explained variation following the *PDSI*. As these two factors are strongly intercorrelated (Table 2) after including *PDSI* in forward selection the proportion of *humus* on explaining the residual variation was reduced to such an extent that it failed in significance testing. Similar is the situation of *pH* and the proportion of fine soil particles (< *0.002*) that also can be considered to be of secondary importance in the studied communities. The complex environmental factor *xericity* (revealed along the first axis of DCA) includes all these intercorrelated effects of both primary and secondary factors. It can be characterised as a gradient of increasing solar irradiation, pH, and soil skeleton content and decreasing content of both humus and fine soil particles. Nevertheless, the solar irradiation keeps its major role as it limits directly species distribution and abundance by extreme drought and high temperatures during the summer period.

Effects of environmental factors in different vegetation types

The individual vegetation types determined by cluster analysis were analysed separately to estimate the effect of environmental variables in each of them. Because of small number of samples in analyses the results should be taken as approximate. At the same time, analyses were performed for both the southern and the northern slopes to find the relevant environmental factors after the influence of aspect is excluded.

In each vegetation type the species data variation was conditioned by the only significant factor: *0.1-2.0* in cluster A, *slope* in cluster B, *soil depth* in cluster C and *PDSI* in cluster D. The floristic composition at the most xeric sites of the *Poo-Festucetum* (B) is thus significantly affected by slope which fluctuates here rather strongly (Fig. 1a). Steep slopes multiple the xericity of microhabitats by increasing erosion and accelerating the drain of rain water. At the same time the chance for plants to establish and survive is reduced. At the least xeric sites of the *Carici-Seslerietum* (D) the *PDSI* seems to play a leading role. It seems that here the solar irradiation may become a limiting factor with respect to its insufficiency rather than its surplus. In both clusters representing the *Festuco-Caricetum* (A and C) soil properties seem to be of the major importance: its depth (*soil depth*) and the soil skeleton content (*0.1–2.0*).

In analysis of the southern slope as a whole where all quadrats are exposed to intensive solar irradiation three factors passed the forward selection: *soil depth*, *humus* and *pH*. The occurrence and frequency of species in xeric conditions will thus depend on the depth and quality of soil. On the northern slope the most important factor passing the forward selection was *PDSI* followed by *soil depth*. This supports the presumption of Sillinger (1931) according to which the overall most important factor is the aspect but on the northern slopes the vegetation composition is also affected by soil depth. On steeper slopes the soil is reduced inducing thus high xericity in top parts of ridges. In the whole region the effect of these two environmental factors is more profound than the effect of altitude which is nowhere evident. The ridge line thus represents a sharp vegetation boundary (cf. Sillinger, 1931; Maglocký, 1979).

Effects of environmental factors upon cryptogams and phanerogams

The effect of environmental variables upon the cryptogams and phanerogams seems to be different. As expected, the vascular plants are controlled by the same factors that were confirmed to be relevant for the whole species set: *PDSI*, *soil depth* and *slope*. In cryptogams, *PDSI* plays obviously a minor role and *soil depth* together with *slope* are the major factors affecting their distribution.

As the lichen species are distributed mostly in extremely xeric sites with shallow and stony soil, it was suggested that they are outcompeted from deeper soils by competitively stronger vascular plants. This suggestion was supported by analysis with included *cover* as a biological explanatory variable. It emerged to be the most relevant factor followed by humus content and the physical soil properties (*0.1–2.0*). Most lichens present belong to the competitively week species occurring prevailingly on carbonatous soils with open vegetation. The analysed stands represent the *Toninio-Psoretum decipientis* (Kotlaba, 1995). The vegetation cover rather than the intensity of solar irradiation seems to be the limiting factor affecting the distribution of lichens. The typical example is *Fulgensia fulgens* occurring at the most extreme sites within the *Poo-Festucetum* (cf. Fig. 2d). This may be possible by the special metabolism of certain lichens representing the type of very effective water-stress adaptation strategy.

The low correlation between bryophyte and vascular plant vegetation has been reported in several vegetation types (review published by Slack, 1984). Herben (1987) suggests the explanation of different behaviour of bryophytes and vascular plants. According to him grassland bryophytes have an opportunistic strategy and respond to factors of much shorter duration and greater fluctuations than vascular plants. Grasses dominating the grassland communities with large underground organs respond slower to environmental factors thus reflecting more conveniently the long-term ecological regime of the stand. On the other hand, the evergreen bryophytes without underground organs may respond very quickly to environmental change (e.g. moisture) and exhibit greater fluctuations. According to Herben (1987) there is a considerable evidence that bryophyte growth is controlled mostly by moisture conditions which may change greatly from year to year. In the studied grasslands the cryptogam abundance in general fluctuated significantly between seasons reaching maximum in autumn and spring.

Gradient analysis and spatial pattern

The results of the gradient analysis is influenced by the size of basic sample units. This was chosen 0.5 by 0.5 m to record the microtopographical heterogeneity of the habitat. The described plant communities sensitively reflect the environmental conditions by their distribution on the southern slope, the plateau and the northern slope. In case of terrain irregularities a mosaic with distinct patches is formed with rather sharp boundaries (cf. Pivničková, 1973). This mosaic of various plant communities represents the coarse grain in spatial pattern of dry grasslands. The diameter of patches in a mosaic may have several meters up to tens of meters. Along the transect different vegetation types changed after 5 to 8 m.

Within the distinct communities the spatial pattern is determined mostly by the microtopographical conditions or by the sociological relationships between the present species. Spatial pattern analysis of *Festuca pallens* (Janišová, unpubl.) showed that the finest grain aggregations corresponding to the morphological pattern of *Festuca pallens* (size of tussocks and their aggregations) have diameter of 10 to 20 cm in the *Poo-Festucetum* or up to 40 cm in the *Festuco-Caricetum*. That is less than the size of basic sample unit chosen. On the other hand, gradient analysis could not encounter larger scale pattern of vegetation determined by the topography (e.g. rocky outcrops in the *Poo-Festucetum* that may give rise to clumps with diameter more than 150 cm) or the distribution of *Carex humilis* tussocks (in the *Festuco-Caricetum* clumps up to 1 m in diameter were revealed). The *Carici-Seslerietum* was not studied in details but its spatial structure seems to be rather homogenous given by dominant and rather regularly distributed ramets of *Sesleria albicans*.

The choice of optimum sample size is a broader question and its solution differs for different vegetation types (McIntosh, 1967). In our case smaller sample units were chosen to reflect the vegetation change at a micro scale. Vegetation boundaries are better detectable using smaller sample units (cf. Pivničková, 1973) .

The vegetation of individual ecologically distinct patches was rather homogenous with rather constant floristic composition and structure. This was found also by Sillinger (1931) who studied dry grasslands in Tematínske kopce Mts. and by Pivničková (1973) in dry grasslands of Central Bohemia. It suggests that the results found in recent study may be valid generally for dry grasslands in top parts of ridges over dolomite bedrock.

Translated by the author

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Janišová M.: **Vzťahy medzi vegetáciou a prostredím v xerotermných travinnobylinných spoločenstvách.**

Vzťahy medzi xerotermnou travinnobylinnou vegetáciou a faktormi prostredia sme vyhodnotili pomocou analýzy údajov z transektu. Skúmali sme spoločenstvá radu *Festucetalia valesiacae v* Považskom Inovci. Údaje o frekvencii druhov sme zaznamenali pozdĺž transektu umiestneného naprieč hrebeňom v severo-južnom smere tak, aby sme mohli rovnomerne zachytiť vegetáciu južného svahu, vrcholovej plošiny a severného svahu. V základných štvorcoch transektu sme merali deväť faktorov prostredia vrátane topografických, pedologických a biologických charakteristík. Štatistická analýza potvrdila signifikantný vplyv troch faktorov prostredia na diferenciáciu sledovaných vegetačných typov, pričom hlavnú úlohu má intenzita slnečného žiarenia (faktor PDSI). Druhým najdôležitejším faktorom bola hĺbka pôdy, tretím sklon. Komplexný environmentálny gradient – xericitu – možno charakterizovať ako gradient vzrastajúcej intenzity slnečného žiarenia, pH, a obsahu pôdneho skeletu a klesajúceho obsahu humusu a jemných pôdnych frakcií. V analýze južného svahu po vylúčení úlohy expozície možno variabilitu druhových dát vysvetľovať najmä pomocou pôdnych vlastností (hĺbka pôdy, obsah humusu a pH). Na severnom svahu boli najdôležitejšími faktormi intenzita slnečného žiarenia a hĺbka pôdy. Vplyv faktorov prostredia na nižšie a vyššie rastliny sa líši. Cievnaté rastliny sme kontrolovali faktormi, ktoré boli dôležité pri anlýze celkového súboru dát – intenzita slnečného žiarenia, hĺbka pôdy a sklon. U nižších rastlín hrá intenzita slnečného žiarenia menšiu úlohu a limitujúcimi faktormi pre ich rozšírenie sú pôdne vlastnosti spolu s pokryvnosťou vegetácie.