The 50th Symposium of the International Association for Vegetation Science, Swansea University, Wales, UK, 23rd-27th July 2007

Environmental factors affecting dry grassland vegetation in the Western Carpathians and Pannonian region (Central Europe)

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Research objectives:

- to perform classification of 128 relevés of dry grassland vegetation located at foothills of the Western Carpatihans and adjacent Pannonian region and characterise the associations by their species combination
- to study the effect of 16 environmental factors on the vegetation variability
- to investigate the representation of Raunkiaer's life forms (Raunkiaer 1934), bryophytes and lichens for individual associations

Material and methods:

128 phytosociological relevés were sampled in 2005-2006 in Slovakia, southern Moravia, Czech Republic and northern Hungary (plot size 16-25 m^2). The effects of 16 environmental factors (Table 1) measured for each relevé were studied. Initial data analysis to remove outlier relevés was carried out using the CANOCO 4.5 for Windows package (ter Braak & Šmilauer 2002). Species data were log-transformed.

Cluster classification was processed by the program PC-ORD 4 (McCune & Mefford 1999) where Ward's linkage method and the relative Euclidean distance as a resemblance measure were applied. Diagnostically important taxa for the individual clusters were determined by calculating the constancy and fidelity measure of each species to each cluster, using the *phi* coefficient of association (Sokal & Rohlf 1995, Chytrý et al. 2002) in the program Juice (Tichý 2002).

The CANOCO 4.5 package was used for running both indirect and direct gradient analyses. **Detrended correspondent analysis** (DCA) defined major gradients in the spatial arrangement of species of the analysed data set. Average Ellenberg indication values (Ellenberg et al. 2001) for relevés were plotted onto a DCA ordination diagram as supplementary environmental data.

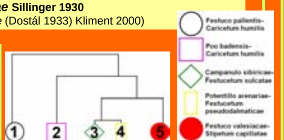
The relationship between species composition and defined environmental factors was analysed over the **canonical correspondence analysis** (CCA). The significance of environmental variables was tested by the Monte Carlo permutation test with restricted permutations (9999 runs). A set of partial CCAs was carried out to quantify the variance partitioned between selected variables (Table 3).

Results and discussion:

1. Classification

Five associations were distinguished in cluster analysis:

Festuco-Brometea Br.-Bl. et Tx. ex Soó 1947
Festucetalia valesiacae Br.-Bl. et Tx. ex Br.-Bl. 1949
Bromo pannonici-Festucion pallentis Zólyomi 1936 corr. 1966
1. *Festuco pallentis-Caricetum humilis* Sillinger 1930 corr. Gutermann et Mucina 1993
2. *Poo badensis-Caricetum humilis* (Dostál 1933) Soó 1971
Festucion valesiacae Klika 1931
3. *Campanulo sibiricae-Festucetum sulcatae* Michalko 1957
(incl. *Cleistogeno serotini-Festucetum sulcatae* Zólyomi 1958, *Festuco rupicolae-Caricetum humilis* Klika 1939)
4. *Potentillo arenariae-Festucetum pseudodalmaticae* Májovský 1955
(syn. *Minuartio frutescentis-Festucetum pseudodalmaticae* (Mikyška 1933) Klika 1938, Art. 3f)
5. *Festuco valesiacae-Stipetum capillatae* Sillinger 1930
(incl. *Alysso heterophylli-Festucetum valesiacae* (Dostál 1933) Kliment 2000)



Diagnostically important species

Treshold criteria:
fidelity of diagnostic species (**Dg**) > 35 %;
constancy of constant species (**C**) > 60 %;
cover values of dominant species (**Dm**) > 25 %.

Cluster 1 - *Festuco pallentis-Caricetum humilis*
Number of relevés: 31
Dg: *Festuca pallens, Fumana procumbens, Linum tenuifolium, Scorzonera austriaca, Leontodon incanus, Helianthemum canum, Carex humilis, Teucrium montanum, Globularia punctata, Stipa joannis, Reseda lutea, Dianthus praecox, Anthericum ramosum, Thymus praecox, Alyssum montanum, Hornungia petraea*
C: *Carex humilis, Sanguisorba minor, Festuca pallens, Teucrium montanum, Linum tenuifolium, Alyssum montanum, Thymus praecox, Euphorbia cyparissias, Arenaria serpyllifolia, Potentilla arenaria, Anthyllis vulneraria, Anthericum ramosum, Teucrium chamaedrys, Helianthemum ovatum*
Dm: *Carex humilis, Stipa joannis, Festuca pallens, Potentilla arenaria, Stipa pulcherrima*


Hainburger Berge, Austria

Cluster 2 - *Poo badensis-Caricetum humilis*
Number of relevés: 22
Dg: *Lactuca perennis, Asplenium ruta-muraria, Sempervivum marmoreum, Digitalis grandiflora, Allium flavum, Verbascum lychnitis, Pseudolysimachion spicatum, Polygonatum odoratum, Pulsatilla grandis,Trifolium alpestre, Stipa pulcherrima, Primula veris, Taraxacum* sect. *Erythrosperma, Ajuga genevensis, Linaria angustissima*
C: *Teucrium chamaedrys, Euphorbia cyparissias, Potentilla arenaria, Koeleria macrantha, Allium flavum, Bothriochloa ischaemum, Stachys recta, Helianthemum ovatum, Carex humilis, Salvia pratensis, Hieracium bauhinii, Eryngium campestre, Teucrium montanum, Stipa pulcherrima, Asperula cynanchica*
Dm: *Potentilla arenaria, Carex humilis, Stipa pulcherrima, Festuca valesiaca, Teucrium chamaedrys, Stipa joannis*


Slovenský kras, Slovakia

Cluster 3 - *Campanulo sibiricae-Festucetum sulcatae*
Number of relevés: 23
Dg: *Festuca rupicola, Carex caryophyllea, Chamaecytisus supinus, Avenula praeusta, Salvia verticillata, Plantago media*
C: *Festuca rupicola, Euphorbia cyparissias, Teucrium chamaedrys, Sanguisorba minor, Koeleria macrantha, Asperula cynanchica, Potentilla arenaria, Eryngium campestre, Centaurea stoebe, Arenaria serpyllifolia, Scabiosa ochroleuca, Alyssum montanum, Fragaria viridis, Festuca valesiaca*
Dm: *Festuca rupicola, Festuca valesiaca, Potentilla arenaria, Teucrium chamaedrys, Stipa pulcherrima, Carex humilis*


Belianske kopce, Slovakia

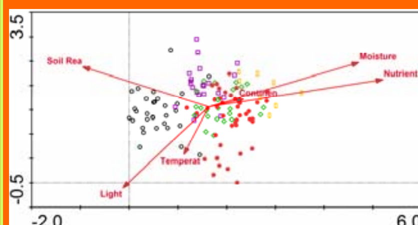
Cluster 4 - *Potentillo arenariae-Festucetum pseudodalmaticae*
Number of relevés: 8
Dg: *Festuca pseudodalmatica, Trifolium arvense, Vicia hirsuta, Potentilla argentea, Lotus corniculatus, Rumex acetosa, Luzula campestris, Picris hieracioides, Achillea nobilis, Cerastium brachypetalum, Daucus carota, Trifolium campestre, Brachythecium glareosum, Galium verum, Poa angustifolia, Carex praecox, Petrorhagia prolifera*
C: *Festuca pseudodalmatica, Sanguisorba minor, Koeleria macrantha, Euphorbia cyparissias, Eryngium campestre, Thymus pannonicus, Poa angustifolia, Lotus corniculatus, Galium verum, Bothriochloa ischaemum, Vicia hirsuta, Trifolium arvense, Teucrium chamaedrys, Hieracium bauhinii, Fragaria viridis, Echium vulgare, Dorycnium pentaphyllum, Centaurea stoebe*
Dm: *Festuca pseudodalmatica, Trifolium arvense*


Börzsöny, Hungary

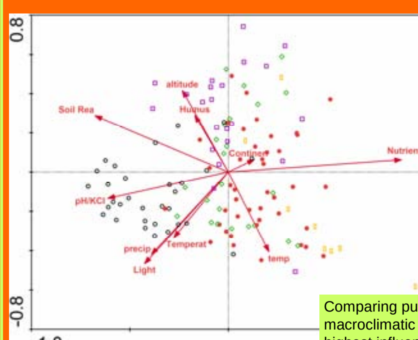
Cluster 5 - *Festuco valesiacae-Stipetum capillatae*
Number of relevés: 42
Dg: *Festuca valesiaca, Erodium cicutarium, Bromus squarrosus, Poa bulbosa, Medicago minima, Asparagus officinalis, Agropyron intermedium*
C: *Koeleria macrantha, Festuca valesiaca, Eryngium campestre, Teucrium chamaedrys, Potentilla arenaria, Euphorbia cyparissias, Thymus pannonicus, Sanguisorba minor, Arenaria serpyllifolia, Stachys recta, Seseli osseum, Centaurea stoebe*
Dm: *Festuca valesiaca, Stipa capillata, Bromus erectus, Teucrium chamaedrys, Stipa pulcherrima, Potentilla arenaria, Koeleria macrantha, Festuca rupicola*


Zoborské vrchy, Slovakia

2. Ordination



DCA ordination diagram of relevés based on average Ellenberg indicator values. Length of gradient 3.53.



CCA ordination diagram of relevés. Only significant variables passing the forward selection are shown.

Table 2. Canonical correspondence analysis					
Axes	**1**	**2**	**3**	**4**	**Total inertia**
Eigenvalues:	0.322	0.209	0.180	0.156	9.502
Species-environment correlations:	0.953	0.932	0.925	0.920	
Cumulative percentage variance					
of species data:	3.4	5.6	7.5	9.1	
of species-environment relation:	21.7	35.8	47.9	58.4	
Sum of all eigenvalues					9.502
Sum of all canonical eigenvalues					1.483

In **canonical correspondence analysis**, 15 variables showed significant marginal effect upon the vegetation (Table 3). Phosphorus did not show significant effect. Surprisingly high number of variables (10) passed the forward selection, explaining only very small percentage of data variability. Nutrients explained 2.9 % of data variability (total inertia); pure effect, after setting all other significant variables as co-variables) reached 1.0 %. Nutrient gradient exhibited the strongest correlation with first CCA axis. Second axis positively correlated with altitude, negatively with mean annual temperature. These two variables in connection with soil reaction explain spatial distribution of relevés assigned into the two studied alliances: *Bromo pannonici-Festucion pallentis* (calcareous dry grassland vegetation on rocky slopes; clusters 1,2) and *Festucion valesiacae* (dry grasslands with *Festuca* sp.div. on deeper soils; clusters 3-5).

Environ-mental variable	Marginal effects	Conditional effects (selection order)	Pure effects
Nutrient	2.9**	2.9 (1)**	1.0**
Moisture	2.7**		0.9**
Soil Rea	2.5**	1.9 (2)**	1.3**
pH/KCl	2.2**	1.3 (6)**	1.1**
precip	1.9**	1.5 (4)**	1.4**
Light	1.9**	1.2 (9)**	1.1**
Temperat	1.8**	1.7 (3)**	1.1**
temp	1.7**	1.6 (5)**	1.4**
altitude	1.5**	1.1 (10)**	1.0**
Continen	1.5**	1.3 (7)**	1.2**
N	1.3**		0.7 ns
humus	1.3**	1.2 (8)**	0.8 ns
Ca	1.2*		1.0 ns
xeric	1.2**		0.9*
inclin	1.2**		1.1**
P	1 ns		

Table 3. Redundancy analysis, results of forward selection.
Marginal effect – percentage variance explained by individual variable while used as the only constraining variable.
Conditional effect – additional variance explained by the variable at the time it was included in the stepwise selection.
Pure effect – percentage variance explained by the variable after all variables significant when alone were used as co-variables (ter Braak & Prentice 1988). Variance explained is shown as % of total inertia.
Legend: ns - not significant, * P<0.05, ** P<0.01

Spatial distribution of alliances. CCA attribute diagrams of relevés: circle size represents species abundance, + - species absence. *Carex humilis* shows distribution of alliance *Bromo pannonici-Festucion pallentis* in the ordination space, while *Festuca valesiaca* represents majority of relevés from alliance *Festucion valesiacae.*

Comparing pure effects of individual variables, the macroclimatic parameters (precip, temp) show the highest influence on data variability (1.4 %). They refer to the geographical location of relevés in E-W direction (contitelality) and altitudinal relations, which affect local flora. Only pH/KCl exhibited a significant effect from the measured pedological parameters. Potential direct solar irradiation (calculated from slope inclination and exposition) did not show any major influence on vegetation variability, since all of the studied associations occur in similar hot S-SW facing sites.

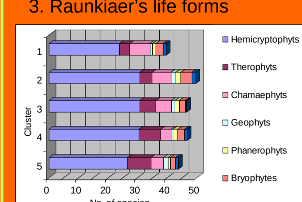
Table 1. Environmental variables used in the analyses

Variable	Variable characteristic [units], source
Macroclimatic parameters	
precip	Mean annual precipitation totals [mm/year], WORLDCLIM database (Hijmans et al. 2005)
temp	Mean annual temperature [°C], WORLDCLIM database (Hijmans et al. 2005)
Pedological parameters	
pH/KCl	Soil acidity
N	Total nitrogen [g/kg of dry matter]
P	Phosphorus [mg/kg of dry matter]
Ca	Calcium [g/kg of dry matter]
humus	Humus [g/kg of dry matter]
Topographical parameters	
atitude	Site altitude [m]
xeric	Potential direct solar irradiation, xericity [%], Jeník & Rejmánek (1969)
inclin	Slope inclination [°]
Ellenberg indicator values (Ellenberg et al. 2001)	
Nutrient	Nutrients
Moisture	Moisture
Soil Rea	Soil reaction
Light	Light
Temperat	Temperature
Continen	Continentality

The relationship between mean Ellenberg indicator values and environmental parameters measured in the field show quite large variation, although we used the Ellenberg indicator values for comparison within the same vegetation type (Wamelik et al. 2002). Comparing the pairs of relevant variables: Soil reaction – pH/KCl and Temperature – mean annual temperature (temp), quite high correlation can be observed. However, the variable pairs do not represent the same environmental characteristics. Mean annual temperature stands for warmth of a geographical area rather than of a specific relevé plot, which is represented by the Ellenberg's temperature value. Strong negative correlation between Continentality and mean annual precipitation totals is obvious. The two associations of *Bromo pannonici-Festucion pallentis* differ in they relationship to the continentality gradient. *Festuco pallentis-Caricetum humilis* is more oceanic, occurring only in the western part of the study area, while the more continental *Poo badensis-Caricetum humilis* is restricted to the eastern part (Slovak and Aggtelek karsts). To interpret weak correlation between Nutrients and humus (which at the same time correlates with altitude) is complicated.

Concluding the results, the studied variables explained only small percentage of data variability. The variability of the studied vegetation types is influenced by numerous partial environmental variables simultaneously. Some other environmental factors, which were not measured in the field, might exhibit principal effect upon vegetation variability (for example soil depth and soil particle size composition, Willner et al. 2004, Mucina & Maglocký 1985). The evolutionary history in postglacial ages has to be taken into account as well (cf. Illyés & Bölöni 2007).

3. Raunkiaer's life forms



We performed a simple evaluation of Raunkiaer's life forms, bryophytes and lichens representation by counting the arithmetic mean for individual associations. Since the studied units represent resembling vegetation types, only small divergence can be observed. The majority of species in the associations are hemicryptophytes (for example grasses). However, difference between the two alliances is obvious. ***Bromo pannonici-Festucion pallentis*** (clusters 1, 2) is typical for higher number of chamaephyts such as short shrubs and succulents. On the other hand, ***Festucion valesiacae*** (clusters 3-5) hosts more therophytes (annuals) in the openings among tussocks. *Poo badensis-Caricetum humilis* (cluster 2) is rich in bryophytes. It is the most diverse association (49 species per relevé plot).

Acknowledgements: we are grateful to all relevé co-authors: M. Zaliberová, J. Kolbek, R. Šuvada, I. Škodová, K. Hegedüšová, E. Illyés, V. Virók, J. Nagy, K. Vidékyová, J. Kliment, J. Májeková, Š. Maglocký, H. Rosinová and M. Dúbravka. The research study was funded by the grant VEGA No. 2/5084/25.